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First biological data, associated fauna, and microclimate preferences of the enigmatic cave-dwelling beetle *Dalyat mirabilis* Mateu, 2002 (Coleoptera, Carabidae)

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Abstract

Dalyat mirabilis is an extraordinary troglobite carabid described in 2002 from the cave Simarrón II in the southeast of the Iberian Peninsula (Spain). A new subfamily Dalyatinae was erected to accommodate this species with remarkable morphological characters and adaptations to live underground. In addition to the former original descriptions, there is only one more study and it aimed to elucidate its evolutionary history. Its closest living relative belongs to the genus *Promecognathus* in North America and both groups seem to have diverged sometime in the late Jurassic to early Cretaceous. In this work, the phenology of *D. mirabilis*, its associated invertebrate fauna and the environmental conditions of the cave Simarrón II were studied for a full year cycle. This carabid is not evenly distributed in the cave, in time or space. It is most abundant during the winter months, wet season, and it disappears from the top layer of the substrate in the summer. A positive correlation was found between the number of carabids captured per trap and the distance to the entrance of the cave; most specimens were captured in traps farthest from the entrance and located in the chamber known as Vias Salas Negras. Furthermore, several spatially-resolved analyses integrating relative humidity, temperature, and the number of captures per trap showed that *D. mirabilis* prefers Vias Salas Negras for having a higher and more stable relative humidity than other chambers in the cave. Larvae were never captured, regardless of intense efforts to collect them for years. Finally, 30 other invertebrate species belonging to 12 different Orders were captured in the cave and are listed here, 25.8%

are troglobites, 29.0% troglophiles and 45.2% troglexenes. The data from this study was used for an initiative to protect this cave and its remarkable fauna. Some of the measures taken by the Administration include the control of human visits to the cave, the installation of a perimetral fence surrounding the entrance, and the installation of an informative panel at the exterior of the cave describing the endemic entomological fauna it contains.

Keywords
Sierra de Gádor, Simarrón II, Spain, troglobite

Introduction

Dalyat mirabilis Mateu (Coleoptera: Carabidae) (Fig. 1) was discovered in the year 2000 in a series of biological explorations of caves in the south-eastern of Spain, in the province of Almería. It was described as a new species in 2002 based on a handful of specimens and a new subfamily Dalyatinae was also erected to accommodate this singular species (Mateu 2002). According to its morphological features, *D. mirabilis* relates particularly to five other members in the subfamily Promecognathinae, one genus is present in North America and four genera in South Africa (Mateu and Bellés 2003). The adaptations to live underground, like the complete absence of eyes and the elongation of appendages (legs and antennae), clearly separates this beetle from its closest relatives in Promecognathinae. A molecular phylogenetic study using 18S rRNA and a fragment of *wingless* concluded that there was a strong support for a sister relationship between the newly erected genus *Dalyat* and *Promecognathus* (genus present in North America). Using a molecular-clock approach the two lineages were estimated to have diverged at a similar age, or slightly earlier than the origin of the subfamily Harpalinae, known to have radiated in the Cretaceous. This is compatible with a vicariant origin of the lineage leading to *Dalyat* because of the isolation of the Iberian plate from Pangea in the late Jurassic to early Cretaceous (Ribera et al. 2005).

D. mirabilis is a true troglobite beetle known from only four locations: Cueva Simarrón II, Cueva de los Chupones, Cueva del Cementerio and an old water mine Fuente Vieja; all of them in Sierra de Gádor (southeast of the Iberian Peninsula). The farthest distance in a straight line between the four locations is no more than 8 kilometers, however these caves are at a very different altitude, with more than 1,000 meters difference in altitude. It has only seen alive and in relatively high numbers in the cave Simarrón-II (Mateu and Bellés 2003). The habitat of *D. mirabilis* and its morphological features, point this species as a strict cavernicole (Mateu and Bellés 2003).

There are only three studies performed on *D. mirabilis*, two morphological descriptions and the molecular analysis that elucidated its phylogenetic origin (referenced above). Unfortunately, nothing is known about the biology, distribution in the cave, environmental requirements, feeding habits, or the population size of this enigmatic species. From a conservation point of view, this information is relevant to take further protective measures in the future.

Figure 1. Adult specimen of *Dalyat mirabilis* (Mateu 2002) in the cave Simarron II.

In the present study, data about the phenology of the species, distribution in the cave Simarrón II, an explanation for the distribution pattern observed, and other arthropods associated with *D. mirabilis* in the cave are described. The new information contributes to the knowledge of *D. mirabilis* in the only cave the species has been found alive in high numbers and it will help prioritize future conservations efforts to preserve this unique species.

Materials and methods

The phenology of *D. mirabilis* and its associated invertebrate fauna was studied in the cavern Simarrón II for a full year cycle, from February to January. Simarrón II is located in the municipality of Dalías, Almería (Spain) at 1,480 m.a.s.l. and in a south-facing slope of Sierra de Gádor. The explored portion of the cave spans for about 453 m (Fig. 2).

Simarrón II was sampled twice per month using dry baited pitfall traps set in the first visit and collected two weeks after. Pitfall traps consisted of a tapered plastic container (8.5 cm diameter at the top) inserted into a cylindrical container of the same diameter. The whole pitfall trap was buried in the soil up to its upper rim and baited with sobrassada (Fig. 3). Sobrassada is a smelly spicy sausage mainly composed of pork fat with some

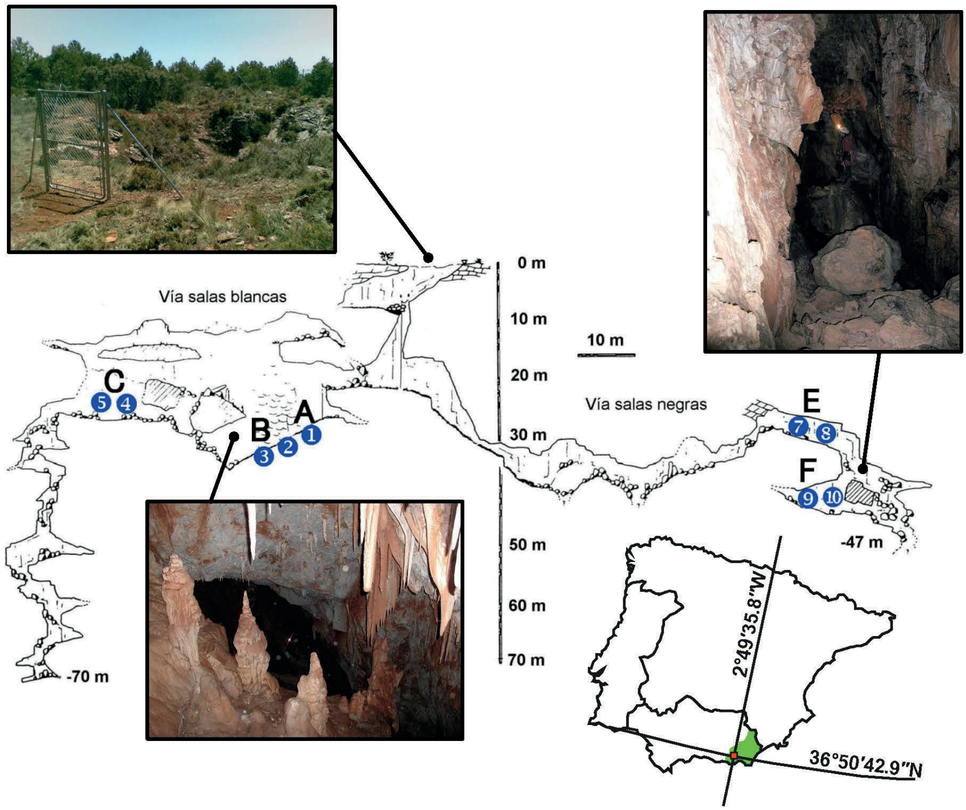


Figure 2. Location of the cave Simarrón-II in Spain, trap numbers and placement locations (numbers in circles) in the cave, as well as temperature and relative humidity measuring stations (letters).

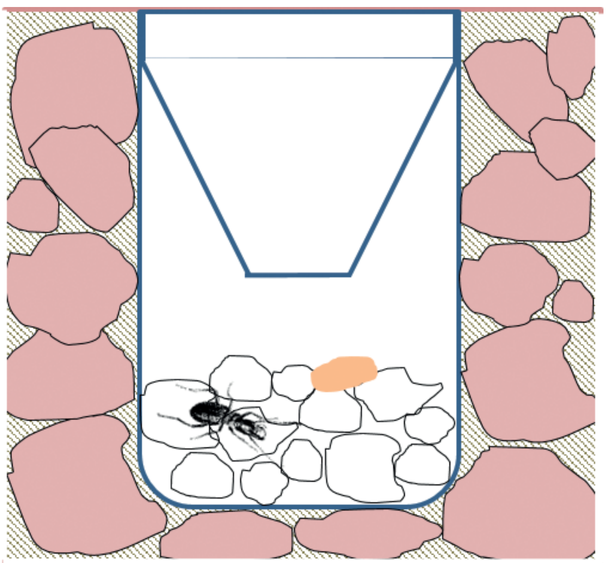
preservatives to avoid fungus and bacterial colonization. It has been shown to be a long lasting and attractive bait for insects (Ortuño and Barranco 2015; Jordana et al. 2017).

Beetles captured alive (Fig. 4) were marked with a unique code using Tipp-ex® and released in the proximity of the trap they were captured. Tipp-ex® was used because is easy to use to mark specimens and dries up in only a few seconds (2–5 seconds). Small rocks were placed at the bottom of the collection chamber of the trap to serve as a refugee to avoid predation among specimens captured. Baited traps were distributed along the cave with an emphasis on the chambers "Salas Vias Blancas" and "Salas Vias Negras" (Fig. 1). Air temperature and humidity were recorded with a HANNA Instruments HI 8564 thermo hygrometer (resolution 0.1 °C and 0.1%, precision range ±0.4 °C and ± 2% RH) in every visit to the cave and at each station with a pitfall trap (Fig. 1). A survey for invertebrates, other than *D. mirabilis*, was conducted in every visit to the cave by direct examination of the substrate, loose rocks, gours, guano, and places with accumulation of organic matter. Around 20–60 minutes were spent sampling the arthropods in the surroundings of each pit fall trap station. Collection of specimens was limited to those necessary for identification.

To explore the distribution of *D. mirabilis*, a single sampling trip to determine the presence/absence of the species during the wet season (highest abundance of the species) was carried out in the caves: Cueva del Cementerio and Cueva de los Chupones (Municipality of Berja), Fuente Vieja (Municipality of Dalías) and Cueva del Águila (Municipality of Berja). All of them are located relatively close to Simarrón II.

The beetle's habitat was characterized in terms of the prevailing temperature and relative humidity of the cave atmosphere Simarrón II. Firstly, the number of specimens of *Dalyat mirabilis* were gridded and interpolated using the inverse distance algorithm. The spatial distribution was represented with a XY Contour Data map using GrapherTM (Golden Software, LLC). The XY coordinates correspond to the cave air temperature and relative humidity, respectively. Secondly, box and bubble plots were used to assess the absence or presence of specimens and its relative abundance in function of the cave microclimate stability.

A



B

Figure 3. Schematic representation of pitfall traps used (**A**) and pitfall traps located in Salas Negras (**B**) during this study to capture live specimens of *D. mirabilis*. Note the rocks and substrate added inside the trap to avoid predation among specimens captured.

Figure 4. Content of one of the pitfall traps after 15 days in the cave Simarron II and containing 6 specimens of *D. mirabilis* (one under the rocks).

Results and discussion

Environmental conditions of Simarrón II

Temperature in Simarrón II was quite stable and the annual averages obtained were 11.7, 11.7, 11.6, 12.0 and 11.9 °C for the sampled stations A, B, C, E and F, respectively (Fig. 5A). Stations A, B, and C correspond to the chamber Via Salas Blancas, and temperatures were slightly colder (~0.3–0.4 °C) than those measured in the stations E and F of Via Salas Negras. The annual fluctuations were 0.13 and 0.19 °C for stations A and B, 0.43 °C for station C, and 0.21 °C for both stations, E and F. The high fluctuations observed in the station C maybe explained by the presence of small cracks at the top of this chamber that connects to the exterior of the cave, as evidenced by organic matter and plant debris found in this area.

The average annual relative humidity (RH) recorded for stations A, B, C, E and F were 81.3%, 82.9%, 86.6%, 90.5% and 91.2% respectively (Fig. 5B). Overall, Via Salas Blancas showed a slightly lower RH (ave = 83.6%) than Via Salas Negras (ave = 90.8%). The annual fluctuations calculated were 9.8%, 10.6% and 7.8% for the sampling stations (A, B, C) in Via Salas Blancas, and 2.0% for stations (E, F) in Via Salas Negras.

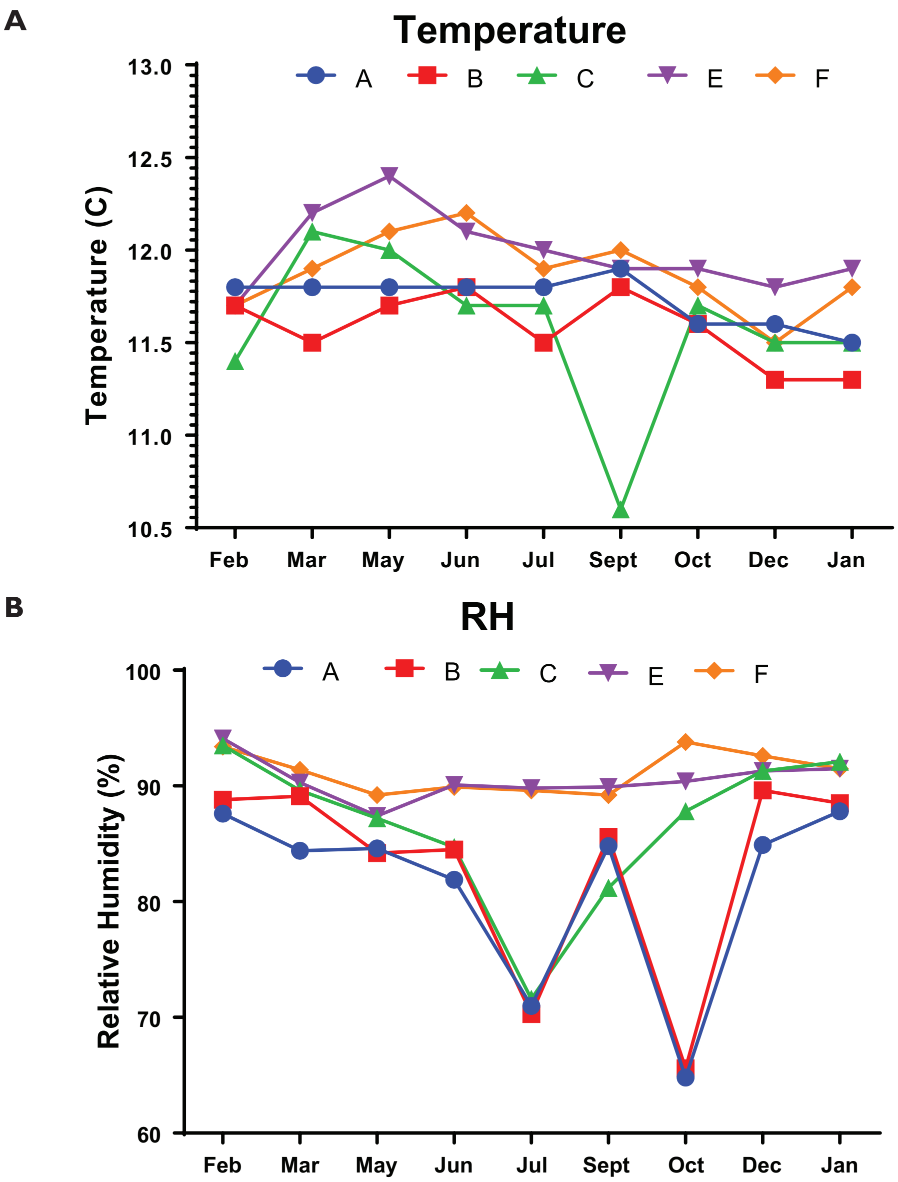


Figure 5. Temperature (**A**) and relative humidity (**B**) data measured at the stations (**A–F**) for a full cycle in the cave Simarrón II.

RH went down to 64.8% during the summer in Via Salas Blancas (station A), while the lowest RH recorded in Vias Salas Negras was 87.4% (station E). The differences between the two areas of the cave are remarkable, and could potentially determine the arthropod-fauna present in each of them. Consistent with a cave located in the Mediterranean basin, humidity decreased in the months of the summer (July-October, dry season) and increased to peak in the months of February-March when the rain and melted snow arrived. In general, during the fall (beginning of the next rainy season of next cycle), the relative humidity increased again to similar levels recorded in previous winter.

Dalyat mirabilis in the cave Simarrón II

A total of 119 specimens of *D. mirabilis* were collected in this study (without counting the recaptures): 89 were captured in pitfall traps and 30 were direct captures. Fourteen specimens were death or predated by other specimens inside the traps. From the carabids captured alive, 53 were marked by a unique code, five were released without taking any action, and 25 were brought to the laboratory for further biological studies. These were sent to the "Departamento de Ciencias de la Vida" in the "Universidad de Alcala de Henares", Madrid (Spain) for feeding, ethological and biological studies. Despite that many of the specimens survived under lab conditions for several months, no mating was observed, and no eggs or larvae could be obtained. Very aggressive behavior was detected among specimens of the same and also opposite sex. Interestingly, *D. mirabilis* uses their mandibles to transport small stones to build a shelter where they remain most of the time. We never observed *D. mirabilis* feeding in its native habitat (cave Simarrón II), but it was previously reported that North American ground beetles of the genus *Promecognathus* prey on polydesmid millipedes (Weary and Will 2020). *D. mirabilis* is a troglobite inhabiting caves exclusively, and millipedes have not been captured in any of the four caves/locations where *D. mirabilis* has been reported. The most abundant and possible prey of *D. mirabilis* in the cave Simarrón-II is the isopod (*Trichoniscus* sp.). Specimens of *D. mirabilis* kept in the laboratory were fed successfully dipteran larvae and the aforementioned isopod.

From the 53 carabids that were marked, only four were recaptured in this study.

The number of specimens of *D. mirabilis* observed at different months and stations sampled in the cave fluctuated widely. The highest number of captures were recorded during the winter months. The number of captures dramatically decreased during the summer months, reaching a minimum in September (only month without captures) (Fig. 6A). The most effective trap was pitfall number 8 (32 captures) and followed by 7 (20 captures), both located in Via Salas Negras. Pitfalls 5 and 9 followed with less than 50% of the captures of pitfall 8 (Fig. 6B). Traps 1 (1 capture) and 2 (no captures) had the least amount of captures, both located in Via Salas Blancas (Fig. 6B).

We explored the possible relationship of the distance of each pitfall trap location to the entrance of the cave and the number of carabid captures obtained per trap (Fig. 7). A direct and positive correlation was found, the highest number of captures were in pitfalls farther away from the entrance (stations F, E and C) (Fig. 7). Pitfall traps 1, 2 and 3 located in stations A and B were the closest to the entrance of the cave and also with the least amount of beetle captures (Fig. 7).

In general, an estimation of the population size of soil arthropods based on using pit-fall traps alone is difficult because it is affected by several factors, including how motile the species subject of the study is. However, several pit-fall traps placed

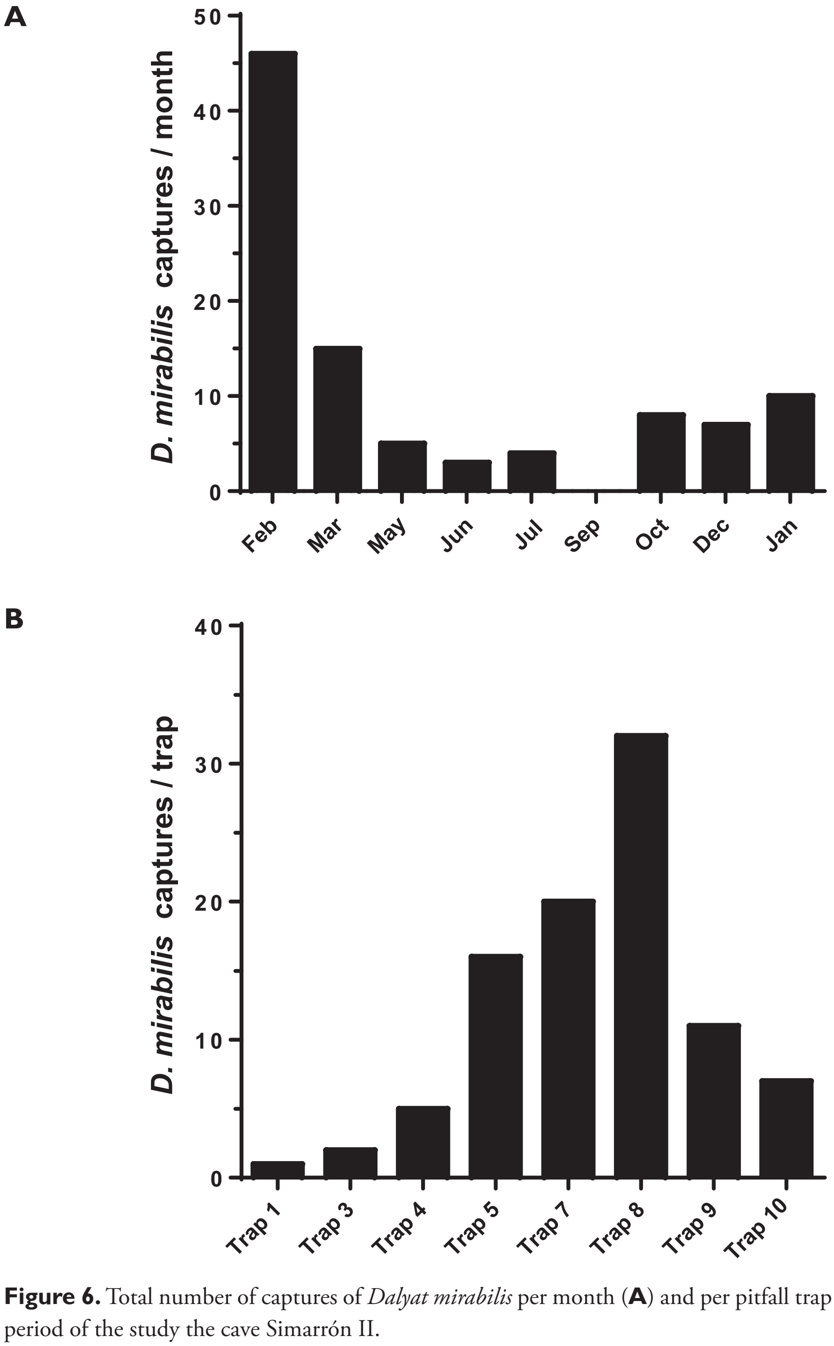


Figure 6. Total number of captures of *Dalyat mirabilis* per month (**A**) and per pitfall trap (**B**) during the period of the study the cave Simarrón II.

strategically on a grid could be used to get an approximation to it (Raworth and Choi 2001). Mathematical models could be used to estimate the population size using properly spaced pit-fall traps distributed using a spatial system in crossed axes (Perner and

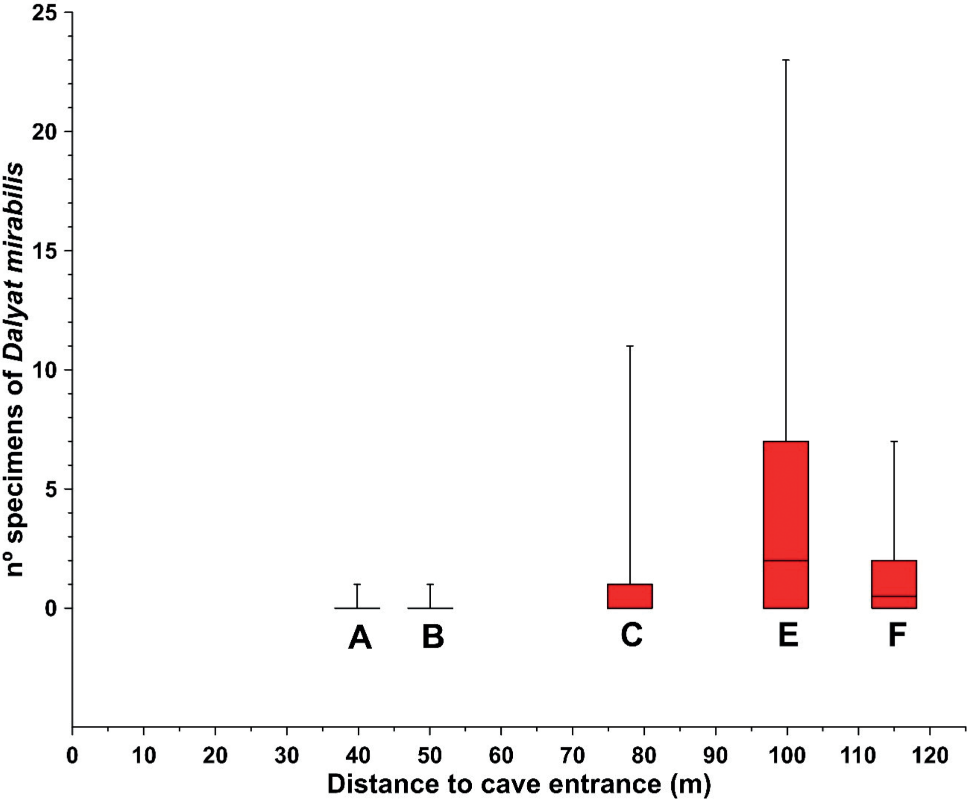


Figure 7. Box-plot representing the abundance and variability of *Dalyat mirabilis* in function of the distance to the cave entrance along each sampling station.

Schueler 2004). The main problem for the design of such a system in a small/medium sized cave is that the possible location of the traps is limited by the development of the cave and the human ability to progress through it. Tercafs and Brouwir (1991) used this method successfully to estimate the population of other cave-dwelling beetles.

Simarrón II has narrow, tortuous and complicated paths, and it is made of large blocks and little or no substrate which makes the placement of traps extremely difficult. Perhaps, this has determined the low number of recaptures in this study, only four specimens in the entire sample period. The low number of beetles recaptured invalidate the application of any formula/models used previously to determine population size, and even if applied, the results would not be relevant using such a low recaptured numbers. It was not optimal that several individuals (14) were found dead in the traps, some live specimens were taken for laboratory experiments (25) and that not all individuals captured alive were marked (5). An observation we made of this species is that it is extremely territorial and aggressive. This may explain the presence of so many dead individuals in the traps (usually body parts); it is a very confined space for several territorial individuals trapped.

There is an important presence of this species in Salas Negras, this is justified by the relatively high number of specimens captured in this part of the cave. However, as mentioned previously, the number of recaptures is low. Other than the explanations given above for this low number, it is also possible that the population size is relatively big, and therefore new "non-marked" specimens are always captured in each sampling trip. This will also imply that the specimens do not "hang around" the area where the trap is located since they are not recaptured, and instead, they keep moving within the interstice of the cave (they are not seeing again). It is an unlikely possibility that marked and released specimens learn to do not fall again in the traps. In any case, future studies will address some problems encountered here and will aim to determine the population size of this enigmatic species.

Environmental conditions of Simarrón II and distribution of *D. mirabilis*

Several spatially-resolved analyses were performed to understand the distribution of *D. mirabilis* in the cave Simarrón II. A distribution map integrating relative humidity, temperature, and the number of captures per trap was created (Fig. 8). This map indicate that the most abundant captures happened in areas of the cave with high relative humidity (>82%), and air temperatures between 11.25 °C and 12.25 °C (Fig. 8). This may indicate that *D. mirabilis* prefers the inner, and most climatically stable areas of the cave, in agreement with the general trend that species richness and diversity of troglobionts are typically greatest deeper inside caves (Kozel et al. 2019).

To further understand the influence of each variable, we analyzed independently whether strong fluctuations in the temperature or relative humidity determine the presence/absence or abundance of *D. mirabilis*. In a first analysis, a strong positive correlation was found for pitfalls with a high number of *D. mirabilis* captured and environmental conditions with a low coefficient of variation (CV) of the relative humidity at those sampling stations. Those stations with the highest number of captures were in areas of the cave with the lowest fluctuations of relative humidity (Fig. 9). We could not find a clear correlation when a second analysis was carried out using the same captures per station and the CV (%) of the cave air temperature. Stations with the highest and also lowest number of captures had relatively stable temperature; however, station C that has the highest annual variation in the air temperature recorded more specimens than station A and B with lowest number of captures but more stable temperature (Fig. 10).

Pitfall traps located in Salas Negras away from the entrance showed more stable environmental conditions: higher and more stable relative humidity compared to Salas Blancas, higher number of captures (% of the total) and a slightly higher and stable temperature (Figs 5, 8, 9 and 10). In fact, this is the only area of the cave that the substrate and walls does not dry out in the summer months; and the environmental conditions (humidity and temperature) favored the presence of *D. mirabilis* all year round. These results suggest that the presence of *D. mirabilis* maybe determined mostly by a high and relatively stable relative humidity. This

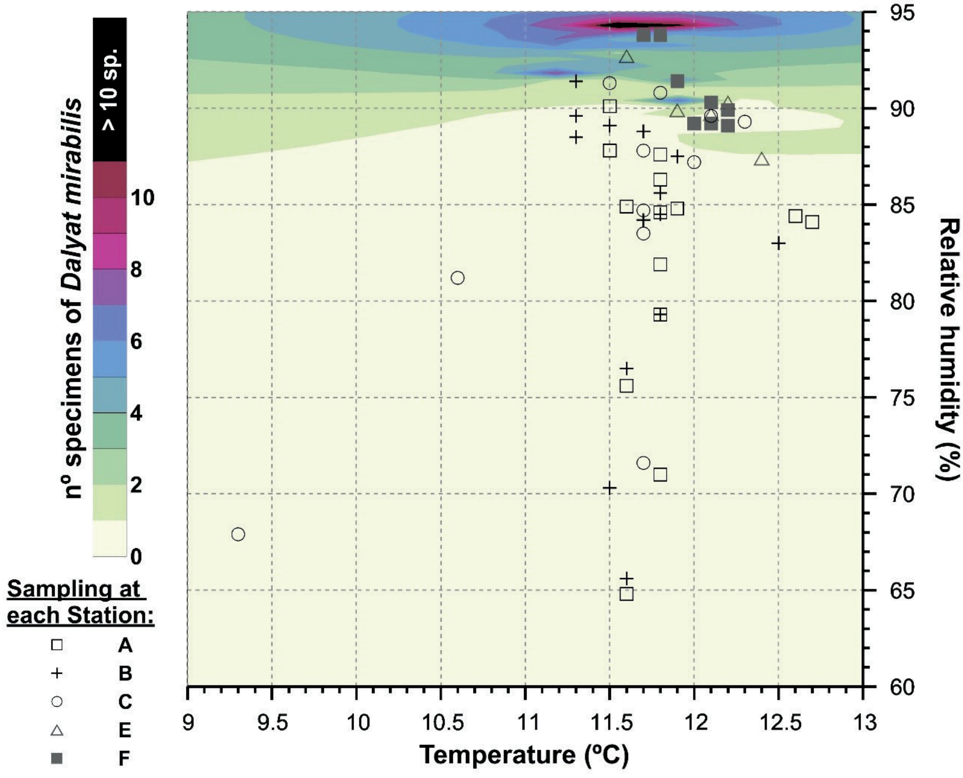


Figure 8. Distribution map for the number of specimens of *Dalyat mirabilis* depending on the cave air temperature and relative humidity. Estimations of the number of specimens are based on the sampling (captures) and temperature and relative humidity records at each station (labelled as **A, B, C, E** and **F**) during an annual cycle, and using the inverse to a distance gridding calculation.

is in line with some early studies on the distribution of cave-inhabiting terrestrial arthropods. It was reported that most abundant populations are usually a short distance inside the dark zone of a cave entrance (Peck et al. 1976). This is where certain microclimatic stability is reached, i.e. contrary to what might be expected, which would be to find a greater species diversity and larger population sizes in the most external parts of the cave with the greatest food availability. A more stable cave environment also favors some species over others; especially species with high specialization for cave life, or edaphic spaces (Tobin et al. 2013; Pellegrini et al. 2016). Other studies suggest that the distribution of several epigeous species (trogloxenes or accidentals) is also linked to cave features (e.g. cave morphology and humidity conditions, among others), and follows patterns that are similar to the ones observed for more usual cave dwellers (Lunghi et al. 2014). Since the temperature was more or less stable across the cave (Figs 2, 5), more studies with a broader range of temperatures are needed to determine the preference of *D. mirabilis*, and its tolerance to seasonal fluctuations.

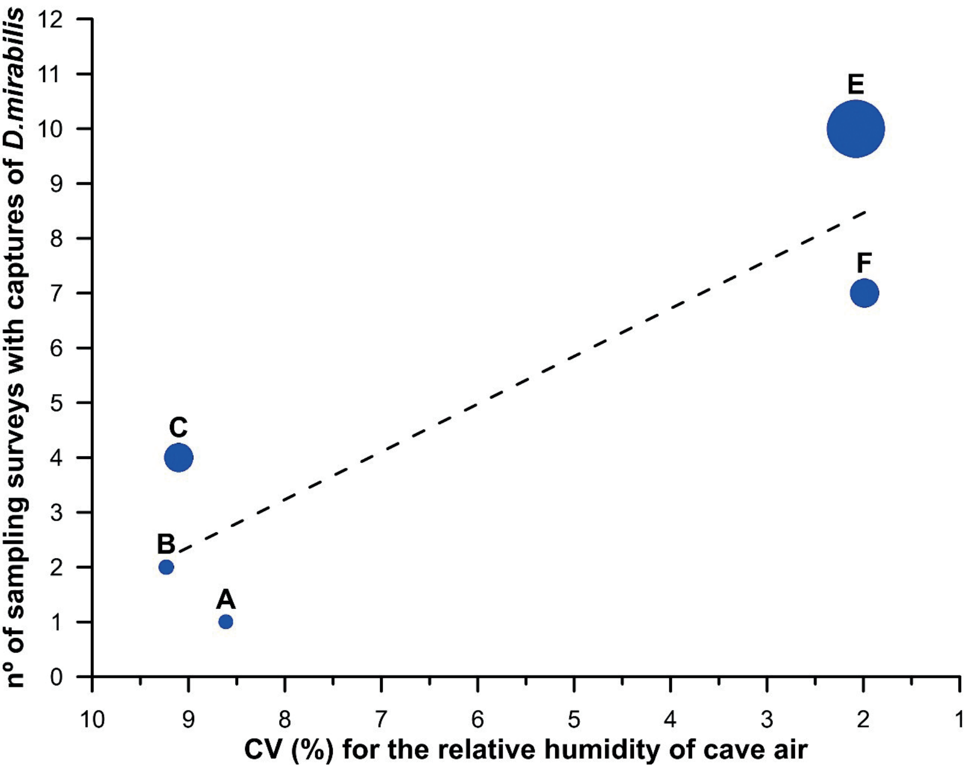


Figure 9. Bubble plot of the presence and abundance of *Dalyat mirabilis* as a function of the coefficient of variation (CV, %) for the relative humidity. The coefficient of variation represents the percentage of the standard deviation to the mean, and it is a useful statistic for comparing the degree of microclimatic stability (in terms of time-variation of humidity) from one location to another into the cave. The size of the blue circles indicates the relative abundance of *Dalyat mirabilis*. The dashed linear function (slope: -0.87, y-axis intercept: 10.20 and R^2 = 0.81) shows a remarkable increment of presence and abundance of *Dalyat mirabilis* as the CV of relative humidity decreases below 3%.

Associated fauna to *D. mirabilis* in the cave Simarrón II

The invertebrate fauna that Simarrón II hosts is unique and with a high level of endemism. A total of 31 invertebrate species were identified in this cave and two are in the process of being described as new species (Table 1). The 31 species includes 8 (25.8%) obligate cave dwellers (troglobites), 9 (29.0%) facultative cave dwellers (troglophiles) and 14 (45.2%) are animals found in caves, but also on the surface, where they encounter proper conditions for their life cycles (trogloxenes).

In addition to *D. mirabilis*, there is another coleopteran of the family Carabidae, *Platyderus speleus*, captured in Simarrón II. This species was originally described from the touristic Caves of Nerja in south Spain (Malaga). It has also been captured in three other caves in the province of Almería (data not published). This is an emblematic species since it is one of two species present in Spain of the genus *Platyderus* that shows a

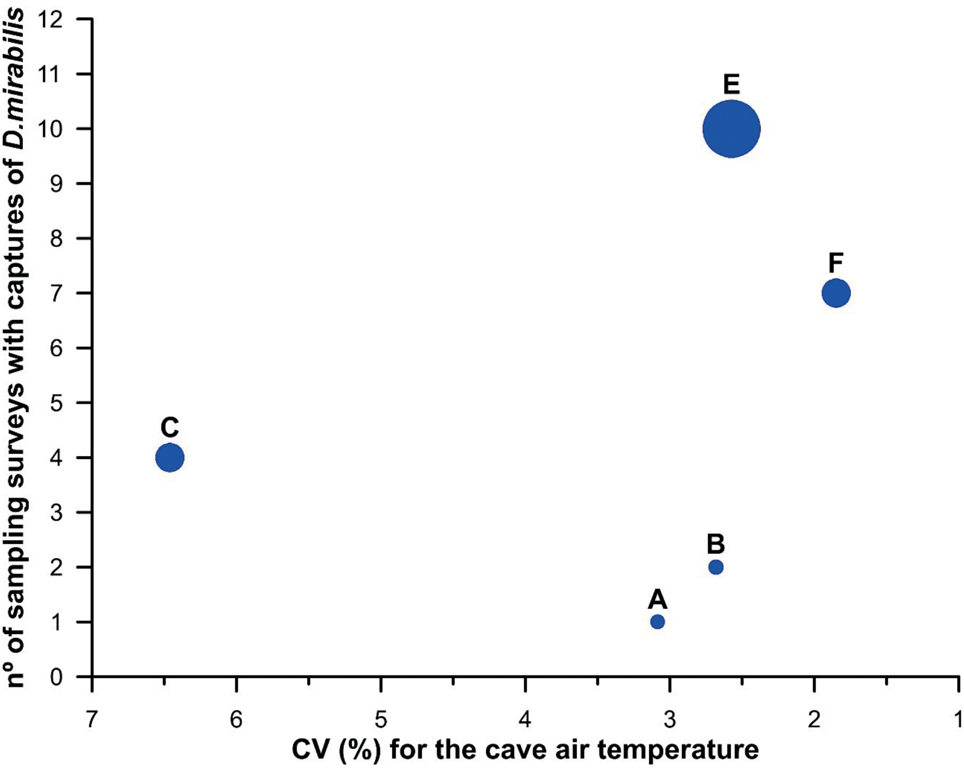


Figure 10. Bubble plot of the presence and abundance of *Dalyat mirabilis* as a function of the coefficient of variation (CV, %) for the cave air temperature. The coefficient of variation represents the percentage of the standard deviation to the mean, and it is a useful statistic for comparing the degree of microclimatic stability (in terms of time-variation of temperature) from one location to another into the cave. The size of the blue circles indicates the relative abundance of *Dalyat mirabilis.*

high adaptation to live in caves (Zaballos and Jeanne 1994), although it can be found outside caves under big rocks too (Anichtchenko 2009).

Potential preys of these two carabids are 8 species of collembolans captured in Simarrón II (Martínez et al. 2004). They are edaphic and troglophiles and distributed along the cave. Some of the species, *Arrhopalites pygmaeus* or *Gisinurus malatestae* are commonly found in the soil in Europe or in Mediterranean countries. *Yoshiiphorura bellingeri* is distinct from other species known and represents a new genera and species described from specimens captured in three caves located at high altitude in Sierra de Gádor (all of them over 1,600 m.a.s.l.). It is a troglophile species, not associated with guano, and it was captured in pitfall traps during all year; however, the number of specimens captured in summer was considerably lower than in the other months.

Two singular species of pseudoscorpions, *Chthonius mayorali* and *Neobisium piquerae*, were captured in Salas Blancas. *Ch. mayorali* was associated with dryer areas in this big chamber, while *N. piquerae* occupied soil and substrate that is permanently wet. In the winter, *Ch. mayorali* was only found in the upper part of the chamber Salas

Table 1. List of arthropod species captured and identified in the cave Simarrón II.

Phylum	Class/Order	Species	Occurrence
ARTHROPODA			
	Insecta		
	Order Coleoptera	*Dalyat mirabilis*	troglobite
		Platyderus speleus	troglobite
		Laemostenus baeticus	trogloxene
		Otiorhynchus sp. nov.	troglobite
	Order Diplura	*Plusiocampa gadorensis*	troglobite
	Order Thysanura	under study	trogloxene
	Order Collembola	*Yoshiiphorura bellingeri*	troglophile
		Mesogastrura ojcoviensis	troglophile
		Acherontiella xenylliformis	troglophile
		Arrhopalites pygmaeus	troglophile
		Onchopodura crassicornis	troglophile
		Gisinurus malatestae	troglophile
		Troglopedetes machadoi	troglophile
		Orchesella cincta	troglophile
	Order Psocoptera	*Psillococus ramburi*	trogloxene
	Order Orthoptera	*Petaloptila barrancoi*	trogophile
	Order Diptera	*Heteromyza atricornis*	trogloxene
		Dixella attica	trogloxene
		Trichocera maculipennis	trogloxene
	Order Siphonaptera	*Leptopsylla taschenbergi amitina*	trogloxene
	Arachnida		
	Order Pseudoscopionida	*Chthonius mayorali*	troglobite
		Neobisium piquerae	Troglobite
	Order Araneae	*Tegenaria herculea*	troblobite
	Order Acari	*Androlaelaps fahrenholzi*	trogloxene
		Eulaelaps novus	trogloxene
		Uroseius acuminatus Dn	trogloxene
		Haemogamasus nidi	trogloxene
		Galeolaelaps helianti	trogloxene
		Proctolaelaps pygmaeus	trogloxene
	Malacostraca		
	Order Isopoda	*Porcellio sp.*	trogloxene
		Trichoniscus sp. nov.	troglobite

Blancas flowstone, probably displaced by *N. piquerae*, that is normally spotted and captured in the lower portion of this space. They are both endemic of Sierra de Gádor and *C. mayorali* has being captured in two other caves, and *N. piquerae* has been reported only from one more cave (Cueva de la Corraliza) where both species also coexist.

The isopod *Trichoniscus sp*. is very abundant in the deepest chamber of Salas Negras all year round, especially in a pile of fresh bat guano where traps 9 and 10 are located. *Trichoniscus sp*. was captured in traps but also by hand capture. Predation on this species by *D. mirabilis* has been observed in the laboratory. This isopod will be described as a new species.

The only identified spider, *Tegenaria aff. herculea* shows troglomorphic adaptations, such as eye size reduction, elongation of appendages and depigmentation (Ribera et al. 2000).

There are two other endemic species captured in Simarrón II that are widespread in other caves in Sierra de Gádor. The first one is the cricket *Petaloptila barrancoi* that has been captured in more than twenty caves in these mountains (Barranco and Amate 2008). It is a troglophile species (Barranco and Molina-Pardo 2021) that does not usually go deep in the cave, and it was only found in the chamber Salas Blancas in Simarrón II. The second species is the dipluran *Plusiocampa gadorensis*, a troglobite species captured along the entire cave of Simarrón II (Sendra et al. 2020). It has also been captured in 10 more caves in Sierra de Gádor: Cueva de la Mudica, Sima Termal, Cueva and Sima del Llano de la Montés, Cueva de la Corraliza, Cueva Nueva, Sima del Aire, Sima del Puntal, Cueva de las Colmenas-II and the artificial water mine Fuente Vieja (data not published).

The flea *L. taschenbergi amitina* is a common parasite of species of rodents in the genus *Apodemus* (Gómez et al. 2013); mice have been observed at the bottom of the entrance shaft during our visits to the cave.

Final remarks

From a faunistic point of view, Simarrón II is arguably one the most interesting caves in Andalusia and probably in Spain, especially because of the presence of *D. mirabilis* in it. This species was captured (in extremely low numbers, sometimes just one specimen) in the relatively nearby Cueva del Cementerio, Cueva de los Chupones, and Fuente Vieja. Therefore, Simarrón II contains the largest known population to date of this enigmatic carabid species. Its presence in four other locations indicates a broader distribution of the species, although it is still restricted to the southwestern portion of Sierra de Gádor since it was not found in any of the north-facing caves sampled. Instead, another enigmatic endemic troglobite carabid species, *Tinautius exilis* Mateu, 2001 has been described from the caves in the northern slopes of this mountain range. A total of 32 caves have been surveyed in Sierra de Gádor and only 4 of them (12.5%) host *D. mirabilis*; this is remarkable if we consider that other caves are ecologically similar and suitable for this species.

The results obtained in this study suggest that *D. mirabilis* prefers areas of the cave with elevated and stable relative humidity all year round. In Simarrón II, these conditions happen in those chambers farthest from the entrance of the cave, and away from the drastic fluctuation of the exterior: freezing temperatures and snow in the winter, and very hot and dry summers. Even in the stable conditions registered in this study for some chambers of the cave, *D. mirabilis* disappears from the main galleries of the cave and no captures were recorded by the end of the summer. It likely seeks refugee in the micro spaces of the cavern until the first rain arrives at the beginning of the fall season. Besides seasonal changes in the local and the cave climate, the spatial distribution of *D. mirabilis* seems to mainly respond to changes in drought intensity between the cave galleries. This is probably the most important factor triggering the migration of this species and its settlement in a more isolated cave site as Salas Negras. It is far from the influence of the seasonal drops of humidity levels registered in microhabitats nearest to the surface and other well-ventilated areas of the cave. This ecological behavior allows us to consider *D. mirabilis* as a likely indigenous hypogean species that mostly avoids droughts, accordingly to the classification proposed by Novak et al. (2004). Indigenous hypogean fauna comprises the group of troglobitic and some troglophilous species migrating between the fissure systems and other inaccessible hypogean habitats adjacent to the cave passage and its taxa are very sensitive to constant high level of air humidity.

The results of the current study were presented to the Andalusian Environmental Protection Agency in the South of Spain. These were the base of an initiative to protect this cave and its remarkable fauna. Some of the measures taken by the Administration included the control of human visits to the cave, the installation of a perimetral fence surrounding the entrance (Fig. 1), and the installation of an informative panel at the exterior of the cave describing the endemic entomological fauna it contains. Visits to Simarrón II are only allowed now with a special permit issued by the corresponding Conservation Authorities (Belda et al. 2014). As a result of the studies reported in this work, *D. mirabilis* was included in the list of protected species in Andalusia (BOJA 2012).

Future actions for the conservation of *D. mirabilis* must include a holistic and spatiotemporal study of its populations. This should integrate the conservation and land-use regulation of the entire carbonate outcrop where the four caves with the presence of this species are located, as well as the locally surrounding karst outcrops. In this area of work, although the landscape scale explains better the species composition and distribution, a local scale model in caves suggests the habitat heterogeneity and environmental stability of cave community (as proposed by Ferreira, 2004) as the key parameters to be considered to reliably identify essential features and patterns for conservation and management actions (Pellegrini et al. 2016), for instance when delimiting the species' protection area.

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