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Environmental factors affecting phenology and distribution of *Tentyria* species (Coleoptera: Tenebrionidae) in Doñana National Park (Southern Iberian Peninsula)

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This research focuses on the effect of environmental factors on the phenology and distribution of the *Tentyria* species (Coleoptera: Tenebrionidae) from Doñana National Park (SW Iberian Peninsula). Data are derived from the results of a project carried out 20 years ago, aimed at inventorying the coleopteran of the park. This information provides a framework for comparison with current or future states since the time elapsed is long enough to detect variations. As the classification of *Tentyria* species is complex and controversial, the first aspect to be addressed was the taxonomical verification of the species. Indeed, they were *T. platyceps* Steven., *T. subcostata* Solier., *T. bifida* Bujalance, Cárdenas, Ferrer and Gallardo, and *T. donanensis* Bujalance, Cárdenas, Ferrer and Gallardo. Sampling consisted of 2 years of monthly pitfall trapping, encompassing the surface of the park and adjacent areas. Data on adult seasonal activity and spatial distribution of the species were obtained from the specific abundance in each sampling plot. Phenologically, the 4 species were mainly summer species, with unimodal or bimodal curves depending on the species. The distribution of the species was quite uneven: while *T. donanensis* was ubiquitous, *T. subcostata* was restricted to the southern coastal area of the park, and *T. platyceps* and *T. bifida* were recorded in the northern half, in marshes or inland forests, respectively. Our results also suggest that extreme temperatures may impose major constraints on the spatial distribution of *Tentyria* species, which could affect Doñana's biodiversity in the future scenery of thermal rise linked to climate change.

Key words: Doñana, phenology, Tenebrionidae

Graphical Abstract

Introduction

Currently, the importance of conserving invertebrate biodiversity is a main concern since these organisms dominate almost all environments and provide multiple benefits and services to the ecosystems (Eisenhauer et al. 2019). A main step to promote their conservation is to obtain accurate and updated information on their taxonomy and abundance across spatiotemporal environmental gradients.

Within this context, the present work is integrated into a series of studies conducted to make known the edaphic entomofauna of Doñana National Park (southern Iberian Peninsula) through a Research Collaboration Agreement (21/98) between the University of Córdoba and the Autonomous Organization of National Parks and financed by the Ministry of the Environment (Government of Spain). This article focuses on the presence and distribution of 4 species of the genus *Tentyria* Latreille 1802, very common beetles running through the sand of this singular natural space. Across Mediterranean and Atlantic sandy soils, Tenebrionids are one of the main components of edaphic macrofauna in terms of abundance (Cheli et al. 2021) and constitute a major part of the diet of diverse predators, as reptiles and birds (Bartholomew and El Moghrabi 2018). Observations of patterns in their abundance provide a framework that allows biologists to assess future changes that could hamper the conservation of their local diversity.

The genus *Tentyria* (Coleoptera: Tenebrionidae: Pimeliinae) is one of the best-represented genera of darkling beetles in the Mediterranean Region, both in abundance and diversity, with over a hundred species and subspecies colonizing diverse environments, from desert to more vegetated areas as steppes or forests, but always warm and xeric (Leo et al. 2018). From a morphological point of view, the taxon constitutes a very homogeneous complex of species of medium size (from 10 to 24 mm), showing a very characteristic look (Fig. 1). It is just the uniformity in the habitus of species that makes it difficult the correct assignment of them, controversial and problematic until very recently.

In the most updated classification of the *Tentyria* from the Iberian Peninsula and the Balearic Islands, a complete diagnosis of 31 species and 6 subspecies and a new key for specific identification are given (Bujalance et al. 2023). Prior, Bujalance et al. (2016) addressed the study of the genus *Tentyria* in Doñana N.P., described 2 new species (*T. bifida* Bujalance, Cárdenas, Ferrer and Gallardo 2016 and *T. donanensis*, Bujalance, Cárdenas, Ferrer and Gallardo 2016) and identified 2 more: *T. platyceps* Steven, 1828; *T. subcostata* Solier 1835, but the taxonomic revision was not yet available.

Despite Tenebrionids being one of the principal components of soil fauna in the Iberian coastlines, most of the literature concerns the taxonomy of species. Nevertheless, there are also research addressing other subjects such as biology, life cycles, or ecology (de los Santos et al. 1982, de los Santos et al. 1988, Martín and Seva 1990; Cartagena and Galante 1999, 2003). Extending the area to other zones of the Mediterranean basin, it is worth mentioning the articles of Carpaneto and Fattorini (2001, 2003), Fattorini and Carpaneto (2001), and Fattorini (2008) addressing the ecology and conservation of Tenebrionid communities colonizing Mediterranean dune ecosystems. Very recently Fattorini (2023) has reviewed the adaptations of darkling beetles to Mediterranean dune environments and the impact of climate change on them.

Concerning the genus *Tentyria*, only punctual information, mainly dealing with local presence data, is available (de los Santos et al. 1988, de los Santos 1992, Sánchez-Piñero and Gómez 1995, Salado 1998). In this regard, one exception is the description of the life cycle of *T. platyceps* Steven, 1828 (López-Sánchez et al.1985).

Then again, one of the first issues to approach when analyzing the spatial distribution of co-occurring species in the same area is their

Fig. 1. Habitus of *Tentyria platyceps*.

spatial ecology and life cycles. Overall, the information available on the processes allowing the coexistence of closely related species in well-structured habitats indicates that the occupation of different patches is one of the main mechanisms facilitating the coexistence because of the reduction of competition for resources (Amarasekare 2003). In this context, Tenebrionid communities in Mediterranean sand dunes are also characterized by a very simplified structure, with a high dominance of certain species (Carpaneto and Fattorini 2001). This is the case of *Tentyria* in Doñana National Park. In addition, the differences in species distribution obtained from the local abundance led to the conclusion that the organization of communities is determined by habitat preferences rather than by interspecific competition (Carpaneto and Fattorini 2001, 2003, Fattorini and Carpaneto 2001). Besides, some factors as different daytime activity rhythms have also been suggested for structuring Tenebrionid communities and reducing competition in the case of closely related syntropic congeneric (Fallaci et al. 1994, Fattorini 2008).

In addition, according to Taylor (1984), spatial distribution is one of the main ecological features of species, being a characteristic parameter that segregates species or populations more than other singular properties like growth or reproduction rates, which may vary between generations or throughout the time. Understanding the processes that regulate the spatial distribution of sympatric, closely related and ecologically similar species is of great interest in the case of singular species, such as endemics. The reason is that these processes themselves are very enlightening for defining strategies for their conservation (Brunjes et al. 2009). At this point, it should be remembered that Doñana National Park is a paradigm of conservation in Europe (Martín-López et al. 2011) and that 2 of the 4 studied species are endemic to Doñana.

Another fundamental but less addressed challenge to conserving Doñana's invertebrates regards on what are the effects of climate on their populations. The high dependence on temperature for insects to be active (Bodlah et al. 2023) and the temperature increase linked to the global change could imply significant variations in the distribution patterns of the species (Liu et al. 2023). For this reason, we consider it important to identify whether there are climatic conditions already restricting the spatial distribution of insect species within conservation key spots, such as Doñana's reserve. Moreover, geomorphology (i.e., slope, aspect) and tree cover are important determinants of the distribution of shade and, thus, of extreme temperatures. Therefore, it is important to assess their relationship to the spatial distribution of populations, in order to interpret climatic restrictions for species' populations.

While Doñana is a key spot for biodiversity conservation, it is immersed in a complex of different uses of the territory (Martín-López et al. 2011), which causes conflicts between conservation and economic development linked to the expansion of agriculture, tourism, and urbanization (García Novo and Marín Cabrera 2006). Very recently (2023) mismanagement policies have led to the removal of Doñana National Park from the IUCN international green list (https://inspain.news/donana-national-park-removed-from-prestigious-green-list/). To counteract the effects of this delisting and promote its conservation, it is necessary to highlight its biological value through research aimed at understanding and protecting the natural heritage of the park in terms of biodiversity. Considering the above-mentioned information, we addressed this research with the main objective of providing a snapshot of the presence and distribution of *Tentyria* species in Doñana at the beginning of the 21st century that will provide a reference to assess posterior changes. This study could not be undertaken until valid taxonomic criteria to allow the correct specific identification of the specimens became available.

Concretely, we address the following issues:

1. To describe the distribution patterns of *Tentyria* species in the territory of Doñana National Park.
2. To establish the seasonal activity of these species.
3. To explore the relationships of some environmental variables with the distribution of the species.

Material and Methods

Area of study

Field research was done in Doñana, a natural space cataloged as "National Park" in 1978 and "Reserve of the Biosphere" in 1980 (Anguas et al. 2002). Later, this place was also included in the catalogs of Special Protection Areas for Birds and in the Sites of Communitarian Interest (García-Canseco 2002). The park is situated in the extreme southwest of the Iberian Peninsula, in the

surroundings of the mouth of the Guadalquivir River, among the provinces of Huelva, Sevilla, and Cádiz. Its surface is approximately of 54.251 ha, and geomorphologically belongs to the lower Guadalquivir River basin (Fernández 1982). From the level of the coast inland, the predominant landscape formations are several systems of advancing young dunes, an old and stabilized dune front, and the set of flooding plains that make up the characteristic marshland system. The space occupied by the stabilized dunes confers the whole rolling topography (Ojeda et al. 2005). The climate is Mediterranean subhumid (Suso and Llamas 1993), with long, dry summers and mild, shorter winters. The rainfall is very variable, and the annual average is around 600 mm. The bioclimatic, hydrological, and morphological effects of winds are extremely significant in Doñana, acting as determinant elements of the dune development process (Bujalance 2016).

The main types of vegetation are the following: forests of *Pinus pinea* L.; cleared oak forests with *Quercus suber* L. as prevalent species; formations of *Juniperus oxycedrus* subsp. *macrocarpa* Sm. and bushes of *J. phoenicea* subsp. *turbinate* Guss in littoral dunes; river forests with *Salix atrocinerea* Brot., *Fraxinus angustifolia* Vahl and *Populus alba* L., as well as a high number of shrubs and climbing plants as *Hedera helix* L.; *Smirlax aspera* L. and *Rubus ulmifolius* Schott; xeric shrub of *Halimium halimifolium* L. and several species of Labiateae, Cistaceae and heath scrub of *Erica scoparia* L., *Stauracanthus genistoides* Brot. and *Ulex parviflorus* Pourr (Bujalance et al. 2016). In the southern extreme of the park's area, dense patches with mixtures of *Pistacia lentiscus* L., *Phillyrea angustifolia* L. and *Myrtus communis* L. or of *Corema album* L., *Cistus salviifolius* L., *Calluna vulgaris* L. and *Erica umbellate* L. are very remarkable (Rivas Martínez et al. 1980).

The vegetation maps of the Doñana National Park are available at the following links: https://www.ign.es/web/catalogo-cartoteca/resources/html/023568.html.

https://portalrediam.cica.es/descargas?dir=undefined&path=%2F04_RECURSOS_NATURALES%2F01_BIODIVERSIDAD%2F01_VEGETACION_ECOSISTEMAS%2F03_HABITATS_BIOTOPOS%2F01_ECOSISTEMAS_SINGULARES%2F02_HUMEDALES%2FComplejo_palustre_Abalario%2FDocumentos&openfile=2496990.

In terms of fauna, the most remarkable highlight is its extraordinary diversity as it is a resting place for numerous migratory birds and a refuge area for such emblematic endangered vertebrates as the Iberian lynx (*Lynx pardinus* Temminck) and the Imperial eagle (*Aquila adalberti* Brehm).

Field Methods

From January 2001 to December 2002, the main natural environments represented in Doñana were surveyed. During the first year, 15 sampling stations (1–15 in Table 1) distributed in the different types of environments present in the southern half of the park's surface were sampled monthly. During the second year, another 15 stations (16–30 in Table 1) were also monthly sampled in the northern half of the park. In addition, to complete the collection of faunal data, sampling stations 31 to 40 (Table 1), which were located outside of the systematic monthly sampling routes, were occasionally visited in 2001 (31–35) and 2005 (36–40).

Complementarily, data from 8 localities (41–48; Table 1) situated outside of the park boundaries were also considered. These are located in the basin of the Guadiamar River up to its mouth, in the vicinity of Doñana's marshes, where the occurrence of *Tentyria* species has been constated (Cárdenas and Hidalgo 2006) was also considered.

Sampling consisted of:

1. Active search and capture of specimens in all the sampling stations.
2. Trapping with pitfall traps: The Pitfall method is widely used in ecology for descriptive and functional studies of soil arthropods (Hohbein and Conway 2018). Eight pitfall traps were set in sampling sites 1–30 and 36–40. Each trap consisted of a cylindrical plastic container of 1,000 cc capacity, buried up to the top end, partially covered to prevent flooding, and baited with commercial acetic acid. Ethanol (70%) was used to preserve the specimens once captured. After 10–20 days (depending on the environmental conditions and time of year) the traps were removed. The direct search and manual collection of specimens was carried out both on the day of placement and on the day of removal of the traps.

For ecological typification of the sampling sites, the criterion of Montes et al. (1998) has been followed. Once the sampling stations were located on the ecological map, their respective ecological types at the ecotone scale were assigned. The local names, geographical coordinates, and ecological typification of the sampling sites are listed in Table 1.

Taxonomic Update

Following the taxonomic update by Bujalance et al. (2023), we identified 4 sympatric species occupying the Park's territory: *T. platyceps* Steven, 1828, *T. subcostata* Solier 1835, *T. donanensis* Bujalance, Cárdenas, Ferrer and Gallardo, 2016; and *T. bifida* Bujalance, Cárdenas, Ferrer and Gallardo, 2016.

The most evident morphological features that allow differentiating these species are the following:

Tentyria bifida show the apex of the anal sternite bifid (an exclusive feature of this species).
Tentyria subcostata with subparallel-sided head, truncate or subtruncate epistome, and no discernible tooth; pronotum with bilobed base, not fully bordered. Specimens of smaller average size and very gracile legs.
Tentyria donanensis of larger average size, head with rounded epistome and provide with a barely perceptible tooth; pronotum proportionally large and with the base completely bordered and prolonged backwards. The elytra is wide oval, arched at the base, and very acuminate towards the apex. Gular groove narrow and normally reduced to a central depression.
Tentyria platyceps has a head proportionally large, eyes flattened; episteme triangular or subtriangular, and provided with a conspicuous tooth; gular groove broad, very wide, deep, well delimited at each side.

Data Analysis

To statistically check phenological differences in abundance between species and across months, we fitted mixed models (Harrison et al. 2018) considering month and species as fixed factors and year as grouping factor. Specifically, we used the Akaike information index (Vrieze 2012) to compare 4 models that represent different possibilities for year-round variation in abundance: (i) a model including a statistical interaction between species and month, representing a situation where both the species sampled, and the month of the year would be important to predict the numbers of beetles found in each sampling site. (ii) a model including only month and the grouping variable, representing a situation where particular months would better predict beetle numbers (ex. during spring). (iii) A model informing only the species and the grouping factor, representing a situation where the species sampled, would

Table 1. The local nomination, UTM Coordinates, and ecological typification in the sampling sites

Sampling sites	Local nomination	Geographical coordinates	Ecological tipification
1	Cruz de Domínguez	37°01′20″N 6°32′45″W	Xerophytic scrub
2	Nave Pedro Pérez	37°00′37″N 6°31′26″W	Juniper grove
3	Laguna del Taraje	36°59′09″N 6°29′00″W	Lagoon complex: grassland and rushes
4	Palacio de Doñana	36°59′25″N 6°26′40″W	Marsh, grasses, and reeds
5	Pozo del Puntal	36°57′40″N 6°26′00″W	Marsh, grasses, and reeds
6	La Algaidilla	36°57′36″N 6°27′00″W	Pines, reeds, and xeric scrub
7	Cerro de los Ánsares	36°60′30″N 6°24′60″W	Inland dunes
8	Corral de la Liebre	36°53′60″N 6°24′34″W	Inland dunes
9	La Vera	36°51′26″N 6°23′34″W	Marsh, grasses, and reeds
10	Mancha Grande	36°51′23″N 6°22′40″W	Pine forest and Juniper grove
11	Palacio de Mariquillas	36°50′19″N 6°22′31″W	Anthropic environment
12	Chozos del Pinar del Faro	36°54′10″N 6°21′00″W	Pine forest and Juniper grove
13	Nave Inglesillo	36°51′00″N 6°24′09″W	Juniper grove
14	Playa de Castilla	36°52′23″N 6°25′19″W	Coastal dune
15	Playa de Castilla 2	36°56′08″N 6°28′17″W	Coastal dune
16	Retuertos	36°59′25″N 6°27′00″W	Marsh, grasses, and reeds
17	Pinar de San Agustín	36°59′24″N 6°27′09″W	Pine forest, heather, and gorse
18	Nido del Gato	37°00′92″N 6°27′33″W	Hygrophilous scrub
19	Santa Olalla	36°58′58″N 6°28′17″W	Lagoon complex: grassland and reeds
20	Las Mogeas	37°02′24″N 6°31′00″W	Pine forest and xeric scrub
21	Camino de Sanlúcar	37°06′50″N 6°28′17″W	Eucalyptus forest and hygrophilous shrub
22	Soto Chico	37°06′23″N 6°28′38″W	Riparian forest
23	Los Monteruelos	37°04′18″N 6°25′14″W	Eucalyptus forest and hygrophilous shrub
24	Casa del Manecorro	37°07′18″N 6°29′10″W	Xeric scrub
25	Boca del Lobo	37°07′99″N 6°29′21″W	Marsh, grasses, and reeds
26	Matas Gordas	37°07′18″N 6°25′45″W	Mastics and cobs
27	Casa de la Pichiricha	37°07′33″N 6°27′09″W	Cork oak grove and kermes grove
28	El Rincón	37°08′15″N 6°30′35″W	Riparian forest and cork oak grove
29	Charco de la Boca	37°07′49″N 6°30′08″W	Grassland and inland dunes
30	Arroyo de la Rocina	37°09′48″N 6°36′23″W	Riparian forest
31	Playa de Malandar	36°47′44″N 6°21′21″W	Coastal dune
32	Desemb Guadalquivir	36°47′05″N 6°20′58″W	Intertidal plain (mouth of the Guadalquivir River)
33	Camino de Moguer	37°08′29″N 6°31′46″W	Riparian forest
34	Gasolinera "El Rocío"	37°01′11″N 6°33′38″W	Anthropic environment
35	Casa del Martinazo	37°01′28″N 6°26′27″W	Marsh, grasses, and reeds
36	Caño Mayor	37°08′03″N 6°25′22″W	Marsh, grasses, and reeds
37	Cercado de las Gangas	37°01′54″N 6°26′39″W	Marsh, grasses, and reeds
38	Pico del Muro	37°07′14″N 6°25′01″W	Riparian forest and eucalyptus forest
39	Soto Grande	37°05′45″N 6°28′29″W	Riparian forest
40	La Muerte del Camello	37°01′51″N 6°25′23″W	Riparian forest
41	Guadiamar PS1	37°28′09″N 6°12′34″W	Riparian forest
42	Guadiamar PS2-3	37°23′49″N 6° 13′36″W	Riparian forest
43	Guadiamar PT	37°14′46″N 6°15′ 56″W	Anthropic environment
44	Guadiamar PS7	37° 13′15″N 6°14′ 06″W	Eucalyptus forest
45	Biocentro Dehesa	37°14′14″N 6°16′27″W	Oak forest "Dehesa"
46	Biocentro Olivar	37°17′48″N 6°14′40″W	Olive grove
47	Biocentro Pinar	37°15′59″N 6° 13′17″W	Pine forest
48	Biocentro Eucaliptal	37° 14′45″N 6°12′38″W	Eucalyptus forest

better predict the obtained numbers of beetles. If this model is selected, it would represent that differences in abundance among species would be systematic and more important than any existing variation across months. (iv) A null model including the intercept and grouping variable, representing the mean of all sampled beetles within a year. To explore how the environmental variables could explain the abundance and distribution of *Tentyria* species in the study area, environmental information obtained from the different metadata catalogs that include this territory was used. Concretely, the following variables were obtained: maximum temperatures (Bioclim 5), minimum yearly temperatures (Bioclim 2), annual precipitation (Bioclim12), tree cover percentage, elevation, and 2 measures of the relief, slope, and aspect of the terrain. The climatic variables

were obtained from the CHELSA database (Karger et al. 2017), with a pixel resolution of 1 × 1 km approximately. Tree cover was obtained from the Hansen Global database (pixel resolution of 5 × 5 km, Hansen et al. 2013). Elevation, relief, and slope were obtained from a digital elevation model (STRM1 REF; 30 × 30 m resolution; Werner 2001).

First, to discern if there were gradients of coupled variation either in beetle abundance or among environmental variables, 2 Principal Components analyses were performed on both sets of variables. Varimax rotation was used to maximize the amount of represented variation in the obtained principal components, and a maximum of 3 different orthogonal axes were allowed in each dataset.

Second, 3 multiple regressions, using Generalized Linear Models, were fitted to correlate the scores of each PCA axis representing the species' abundance with the 3 axes representing environmental variation has been performed. This allowed us to identify sets of correlated variables capable of predicting changes in the abundance of *Tentyria* species across our study plots. All the analyses were executed using the R Core Team (2020) software, and the scripts are available under request to the authors.

Results

Seasonal Activity

Based on the monthly relative abundance data (number of specimens; Supplementary Table S1), the seasonal activity pattern of each *Tentyria* species inhabiting Doñana has been plotted (Fig. 2).

For the 4 species, summer seems to be the most favorable time, particularly in the case of *T. platyceps* and *T. bifida*, whose catches outside this period were scarce or nonexistent. The suitability of a warmer environment is more evident in the case of *T. bifida*, which was found active only between June and September, with the maximum in July.

Tentyria platyceps, despite being an uncommon and scarce species in the studied area, was found active most of the year except in the strictly winter months, but the activity curve also peaked in July.

Tentyria donanensis, the most abundant species in the area, showed a wide activity period which spreads from February to October, reaching the highest values in summer (July).

Tentyria subcostata behaves as the less thermophilic species: its activity period was shifted towards springtime when the maximum population was observed, but ranged from January to October. It showed intermediate values in summer and can be active even in winter.

Our model selection procedure unambiguously indicated that the full model, including the interaction between species and month of the year, was the best explaining variation in the number of beetles found at each sampling site. The full model, including an interaction between species and month of the year, indicates positive effects of the month on abundance during spring and summer compared with January, but with different increases in numbers among the 4 species (Supplementary Table S2).

Spatial Distribution

Figure 3 shows the location of the sampling plots where the different *Tentyra* species were found. *Tentyria donanensis,* the most abundant species, was also the most ubiquitous, showing the remaining species showed a more restricted distribution. Concretely, *T. subcostata* was restricted to the southern half of the park, where it seems to be circumscribed to the coastline and the mobile dune front that extends inland. On the contrary, *T. bifida* and *T. platyceps* have only been found in the northern half; the first, in the vicinity of "El Rocio," in the marshland area, and the second one further inland.

Searching for a relationship between the distribution of the species and their corresponding environmental type, it has been found that *T. subcostata* only colonizes coastal or inner dunes, with bare sandy soils or with little psammophilous vegetation (mostly species of the genus *Euphorbia*, *Eryngium*, and *Amnophila*). *Tentyria bifida* seems linked to areas of xerophytic vegetation, with masts (*Pistacia lentiscus*), heather (*Erica*), and kermes (*Quercus coccifera*), also extending to areas with relict cork oaks (*Quercus suber*) and toward the edge of the marsh lands, with grassland (*Tuberaria*, *Plantago*, *Trifolium*) and reed lands (*Juncus*). *Tentyria platyceps* has been found in forested areas further inland, with a vegetation in which mastic grove (*Pistacia lentiscus*), kermes (*Q. coccifera*) and cork oaks (*Q. suber*) as dominant plant species. *Tentyria donanensis*, in contrast with the other species, was observed in virtually all the environmental types (Fig. 3; Table 1).

Relationship Between Environmental Variables and the Distribution of the *Tentyria* Species in Doñana National Park

The PCA of abundance data rendered 3 new axes of species abundance variation, representing 77% of the original variation in the abundance of the *Tentyria* species. PC1 represented variation in the abundance of *T. platyceps* (loading 97%) and *T. subcostata* (loading 77%), PC2 represented variation in *T. donanensis* (loading
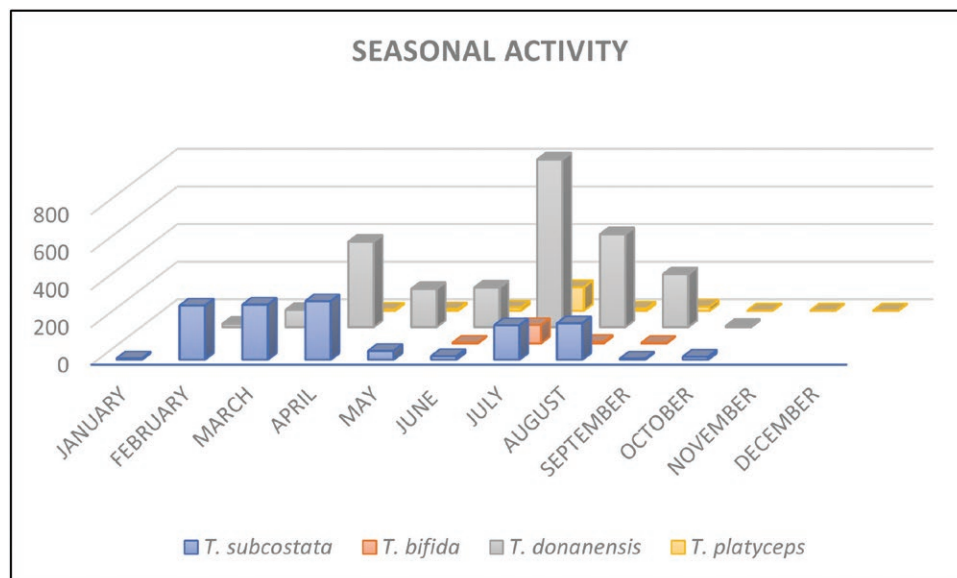

Fig. 2. Seasonal activity pattern of *Tentyria* species.

71%), and PC3 represented variation in the abundance of *T. bifida* (99%) (Table 2).

Concerning environmental variation, the 3 new axes represented 72% of their original variation. PC1 represented *variation in maximum and minimum temperatures* (loadings 98% and 96%, respectively). PC2 represented correlated variation in altitude (loading 82%), tree cover (66%), and precipitation (70%). Finally, PC3 represented variation in slope and aspect of the terrain (loadings 60% and 77%, respectively).

Among the 9 independent correlations evaluated, only the axis of thermal variation was significantly correlated with the variation in the coupled distribution of *T. donanensis* and *T. subcostata* (Table 3).

Figure 4 shows how both species gradually decrease in abundance per plot as maximum and minimum temperatures become more extreme. Our results indicate that extreme temperatures can restrict the presence of *Tentyria* species in the sampling plots: thus, *T. donanensis* and *T. subcostata* gradually decrease their abundance as the thermal environment becomes more extreme, while *T. platyceps* and *T. bifida*, whose abundance is not correlated with the thermal variable, are absent from the thermally hardest plots.

Discussion

Taxonomy represents one of the fundamental supports around which biodiversity is organized and assessed in the field of animal research and conservation (Sandall et al. 2023). Given that the set of species on which our study focuses belongs to a historically controversial genus from the point of view of its specific arrangement, the first step to approach was to check the previous taxonomic classification of the *Tentyria* species inventoried in Doñana National Park (Bujalance et al. 2016) in the light of the most recent literature (Bujalance et al. 2023). After verification of this point, the list of *Tentyria* species inventoried in Doñana proved to be valid. Accordingly, we have been able to establish the spatial distribution of these species in the area.

Here, we provide reference information on the phenology and spatial distribution of *Tentyria* species in Doñana. From it, variations in the presence and distribution of species could be assessed in the future and related pressing issues, such as climate change or anthropization.

Regarding their phenology, *Tentyria* species of Doñana exhibit a thermophilic condition, as their activity (maximum abundance of adults) peaks in the warmest month (July). Adaptations to survive in arid environments involving the species' life cycles are habitual in darkling beetles (Fattorini et al. 2023). In this regard, darkling beetles inhabiting Mediterranean coastal areas often show the adults' abundance peak in autumn, supposedly because water availability could be limiting adult survival in summer, Fattorini (2008). Nevertheless, in our study, 2 phenological patterns have been observed: first, *T. platyceps*, *T. donanesis*, and *T. subcostata* whose adults displayed a broad phenological pattern, being active throughout most of the year. Among them, *T. platyceps* appeared more skewed towards the autumn. Second, adults of *T. bifida* were constrained to summer months.

The first patterns partially agree with those of Cartagena and Galante (1999) for the species *T. laevis sensu* Cartagena and Galante (nec Solier) and *T. peiroleri sensu* Cartagena and Galante (nec Solier) from brackish coastal areas of the southeast of the Iberian Peninsula. The course of the abundance of *T. subcostata* fully complies with the pattern described for *T. laevis*, peaking twice: in early spring and at midsummer, while the activity pattern observed for *T. donanesis* fits better to that of *T. peiroleri sensu* Cartagena and Galante (Cartagena and Galante 1999), with a more noticeable maximum in midsummer.

According to these authors, both activity patterns would correspond to 2-year life cycles, characterized by a very long period of activity, in which reproduction would begin in late spring (first peak of activity) and last until the end of the warm season (de los Santos et al.1988). A long and biannual life pattern has also been described for other Iberian species of the genus, such as *T. elongata* Walt (Martín and Seva 1990), *T. incerta* Solier (Sánchez-Piñero and Gómez 1995), and *T. grossa* Besser (Fallaci et al. 1994).

According to Cartagena and Galante (1999), the pattern obtained for *T. laevis* could be a strategy to avoid unfavorable periods corresponding to intense rainfall or extreme temperatures. To evade extreme temperatures of the inner sandy soils may also be the explanation for the very restricted distribution area of *T. subcostata*, which colonizes exclusively littoral or sublittoral habitats, where climatic conditions are less life-threatening, as too high temperatures become intolerable even for thermophilous species (Fattorini 2023).

The phenology of *T. platyceps* extends from March to October. In accordance with de los Santos et al. (1988), this species could belong to the second type, with larvae overwintering and adults emerging in midsummer. It is worth mentioning that in Doñana we have found active specimens of *T. platyceps* even in December, which suggests a somewhat longer period of activity, in which only the strictly winter months are avoided, and which underlines the importance of the temperature variations in regulating Tenebrionids life cycles. Variations in phenological patterns in response to local climates have been observed for other coastal Tenebrionids. For example, the phenological peak of *Erodius siculus* Solier was observed earlier in Sicily than in the continent and it was associated with the warmer climate of the island (Di Stefano and Fattorini 2000).

Unlike the previous species, *T. bifida* showed a much shorter adult activity period being only captured in summer (June–September). The unique maximum of adults of this species in summer might correspond to a "one-year life cycle," with overwintering larvae and spring-emerging adults (de los Santos 1988). Yet, in our study, *T. bifida* emergence was somewhat delayed.

In short, the phenological patterns observed among Doñana's *Tentyria* species agree with Fattorini (2023) statement that Tenebrionids' life cycles in Mediterranean dunes are tuned to temperature changes. Besides, in agreement with Draney (1993), the skew toward the autumn observed in *T. platyceps* might help this species reduce its exposure to competition with the others.

Regarding spatial patterns of *Tentyria* species in Doñana, our study shows different distribution areas of the 4 *Tentyria* species present in Doñana: *T. donanensis*, ubiquist; *T. subcostata* only found in the coastline, in the south of the park; T. *platyceps* and *T. bifida* were recorded in the marshlands and inland areas, respectively. To explain these spatial segregations of so closely species, we made a first exploratory analysis of how environmental gradients may relate to the presence of *Tentyria* species in Doñana considering different environmental. Our results suggest that both hot and cold extreme temperatures might be constraining their spatial distribution, particularly *T. donanensis* and *T. subcostata* (Fig. 4). Furthermore, although the other species' abundance was not linearly correlated with extreme temperatures, these species were also absent from plots with particularly extreme temperatures, either high or low. The most extreme shaded air temperatures found laid between 6.15 °C and 33 °C (Sites 41–48), none of which are particularly extreme for known ranges of arthropods' thermal tolerance, respectively (Khaliq et al. 2023, Camacho et al. 2024). Nonetheless, air temperatures in the shade are tightly associated with much more extreme temperatures co-occurring at the surface of the exposed soil (Camacho et al 2024), which is the typically used microhabitat by our study group. Data

Fig. 3. Spatial distribution of *Tentyria* species in the area of Doñana National Park.

on critical thermal limits are unavailable for *Tentyria* species, but it is known that some darkling beetles can withstand very short exposures to temperatures up to 45 °C (i.e., *Pimelia obsoleta* Solier; Heatwole and Harrington 1989).

Therefore, we propose that the sampling sites reaching the most extreme temperatures in Doñana may reach harmful thermal levels for the local species of *Tentyria* and constrain their local distribution. Given that insects often have their geographic distribution and

Table 2. Results of a model selection procedure to identify best predictors of numbers of Tentyria beetles in sampling sites located within Doñana's National Park and surroundings. AIC: Akaike information criterion

Model	df	AIC	Fixed factors	Grouping factor
m	50	973.7	sp X month	year
m1	14	1315.9	sp	year
m2	6	1382.2	month	year
m3	3	1413.2	intercept	year

Table 3. Effects of environmental gradients on the abundance of *Tentyria* species across the surface of Doñana's National Park. don: *T. donanensis*; sub; *T. subcostata*, plat: *T. platyceps* and bif: *T. bifida*. Prec: precipitation; Elev.: elevation; Cover.: tree cover

	Estimate	Std. error	t-value	Pr(>|t|)	Species
(Intercept)	0.000	0.141	0.000	1	don/sub
temperature	−0.327	0.142	−2.296	**0.0265**[*]	don/sub
prec_elev_cover	0.029	0.142	0.201	0.84	don/sub
relief	−0.015	0.142	−0.106	0.91	don/sub
(Intercept)	0.000	0.147	0.000	1	plat
temperature	−0.016	0.148	−0.110	0.91	plat
prec_elev_cover	−0.183	0.148	−1.239	0.22	plat
relief	−0.043	0.148	−0.287	0.77	plat
(Intercept)	0.000	0.148	0.000	1	bif
temperature	0.049	0.150	0.327	0.74	bif
prec_elev_cover	−0.041	0.150	−0.272	0.78	bif
relief	0.088	0.150	0.584	0.56	bif

Bold is used to emphasize significance in *P* values.
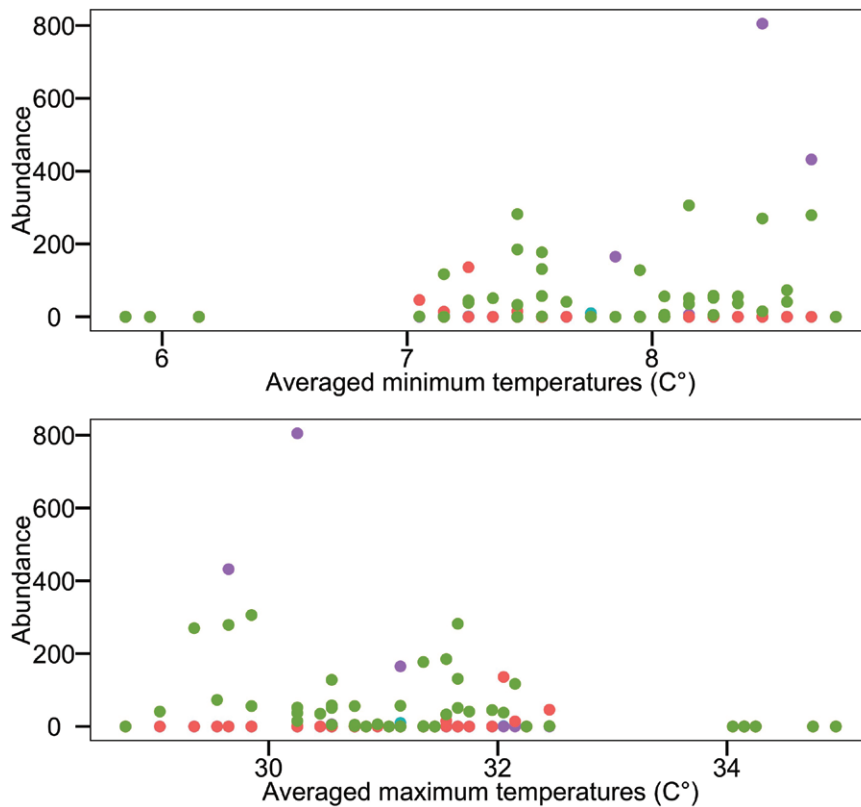
Fig. 4. Distribution of *Tentyria* species in thermal gradients of air temperatures measured in the shade. (Abundance = number of specimens).

abundance constrained by local temperatures (Sánchez-Guillén et al. 2016, Khaliq et al. 2023, Camacho et al. 2024), our results suggest that at least *T. donanensis* and *T. subcostata* might become progressively restricted in Doñana if environmental temperatures become more extreme.

In turn, our results did not support previous claims that vegetation, especially shrub cover, is crucial for habitat selection of darkling beetles at local scales (Liu et al. 2012). Our study region's vegetation cover ranges from sparse shrubs at coastal dunes to forests of pine trees, which are often crossed by open pathways. Therefore, we consider that local vegetation cover did not reach sufficiently extreme levels to constrain the abundance or distribution of the species composing our study group.

Insects are also able to alter their physiology and behavior to try to maintain the body temperature into a range that avoids thermal stress (Lahondère 2023). Particularly, Tenebrionids of arid environments have developed several morphological and physiological adaptations to enduring thermal rigor. For instance, tegument coloration may facilitate thermoregulation because dark-colored species heat up and cool down faster than lighter-colored insects (Rajpurohit et al. 2008, Matthews et al. 2010). Accordingly, dark, or black, colors are common in soil beetle's inhabitants in arid coastal, or desert areas as is the case of *Tentyria* species. Although these species are adapted to survive under stressful hot conditions, they may also be especially vulnerable to slight increases in temperature since they may be enduring a temperature range very close to the limit defining their thermal tolerance (Fattorini 2023).

Given our results, we argue that combining knowledge of thermal tolerance and possibilities of thermoregulation should help explain the spatial distribution of *Tentyria* species in Doñana and predict possible changes in their spatial distribution, as evidenced in other insect groups (Kellermann et al. 2012). There are several alternatives to measure thermal tolerance, such as measuring critical thermal limits using different approaches (Terblanche et al. 2011, Bauerfeind et al. 2018, Leong et al. 2020). Nonetheless, behavioral measures of thermal tolerance, due to being less extreme might provide more power to detect thermal constraints on their spatial distribution, as has happened in other ectothermic animals (Camacho et al. 2023). To obtain meaningful observations of thermal tolerance, it is important to consider plasticity in such measurements and interactions with water availability (Terblanche et al. 2007, Lima et al. 2021). Finally, these estimates should be combined with fine estimations of extreme temperatures at the microhabitats used by the species (Camacho et al. 2015, Kearney and Porter 2020) to observe or predict thermal constraints on the species' spatial distribution.

The findings of our study raise several questions to be addressed: (i) To know the current status of *Tentyria*'s populations in Doñana, as the time elapsed since the initial data collection is wide enough to assess changes to be interpreted from the perspective of global change. (ii) To know the thermal tolerance and capacity for thermoregulation of *Tentyria* species in Doñana through laboratory experiments and field observations. That would allow us to mechanically model the effects of climate change on these species and their impact on the food chain, of which they are a main component.

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Author contributions

Ana María Cárdenas Talaverón (Conceptualization [Equal], Data curation [Equal], Methodology [Equal], Writing – original draft [Equal], Writing – review & editing [Equal]), José Bujalance (Investigation [Equal], Supervision [Equal], Writing – review & editing [Equal]), and Agustín Camacho (Data curation [Equal], Formal analysis [Equal], Investigation [Equal], Supervision [Equal], Writing – review & editing [Equal])

Supplementary data

Supplementary data are available at *Journal of Insect Science* online.

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References

Amarasekare P. 2003. Competitive coexistence in spatially structured environments: a synthesis. Ecol. Lett. 6(12):1109–1122. https://doi.org/10.1046/j.1461-0248.2003.00530.x

Anguas JM, Carmona JJ, Isendahl N, et al. Directorio de organizaciones ambientales de la comarca de Doñana. Madrid, Spain: WWF/ADENA; 2002. p. 258.

Bartholomew A, El Moghrabi J. 2018. Seasonal preference of darkling beetles (Tenebrionidae) for shrub vegetation due to high temperatures, not predation or food availability. J. Arid Environ. 156(1):34–40. https://doi.org/10.1016/j.jaridenv.2018.04.008

Bauerfeind SS, Sørensen JG, Loeschcke V, et al. 2018. Geographic variation in responses of European yellow dung flies to thermal stress. J. Therm. Biol. 73(1):41–49. https://doi.org/10.1016/j.jtherbio.2018.01.002

Bodlah MA, Iqbal J, Ashiq A, et al. 2023. Insect behavioral restraint and adaptation strategies under heat stress: an inclusive review. J. Saudi Soc. Agri. Sci. 22(6):327–350. https://doi.org/10.1016/j.jssas.2023.02.004

Brunjes KJ, Ballard WB, Humphrey MH, et al. 2009. Home ranges of sympatric mule deer and white-tailed deer in Texas. Southwest. Nat. 54(3):253–260. https://doi.org/10.1894/md-06.1

Bujalance JL. 2016. Estudio taxonómico y ecológico de los Tenebrionidae (Coleoptera) del sureste de la Península Ibérica. El caso del río Guadiamar y de Doñana [Tesis Doctoral]. Córdoba (Spain): University of Córdoba (Spain). https://helvia.uco.es/xmlui/handle/10396/13255

Bujalance JL, Cárdenas AM, Ferrer J, et al. 2016. The genus *Tentyria* (Latreille, 1802) in Doñana National Park (Southern Iberian Peninsula) with descriptions of two new species (Insecta: Coleoptera: Tenebrionidae). Ann. Zool. (Waszawa). 66(3):345–355. https://doi.org/10.3161/00034541ANZ2016.66.3.001

Bujalance JL, Ferrer J, Cárdenas AM. 2023. A taxonomic revision of the genus *Tentyria* Latreille, 1802 in the Peninsula and Balearic (Coleoptera: Tenebrionidae). Zootaxa 5320(1):1–88. https://doi.org/10.11646/zootaxa.5320.1.1

Camacho A, Trefaut-Rodrigues M, Navas C. 2015. Extreme operative temperatures are better descriptors of the thermal environment than mean temperatures. J. Therm. Biol. 49–50(1):106–111. http://doi.org/10.1016/j.jtherbio.2015.02.007

Camacho A, Angilletta Jr MJ, Levy O. 2023. A theoretical thermal tolerance function for ectothermic animals and its implications for identifying thermal vulnerability across large geographic scales. Diversity 15(5):680. https://doi.org/10.3390/d15050680

Camacho A, Rodrigues MT, Jayyusi R, et al. 2024. Does heat tolerance actually predict animals' geographic thermal limits? Sci. Total Environ. 917(2024):1-11. https://doi.org/10.1016/j.scitotenv.2024.170165

Cárdenas AM, Hidalgo JM. 2006. Ecological impact assessment of the Aznalcóllar mine toxic spill on edaphic coleopteran communities in the Guadiamar river basin (southern Iberian Peninsula). Biodivers. Conserv. 15(1):361–383. https://doi.org/10.1007/s10531-005-2785-x

Carpaneto GM, Fattorini S. 2001. Spatial and seasonal organization of a darkling beetle (Coleoptera: Tenebrionidae) community inhabiting a Mediterranean coastal dune system. Ital. J. Zool. 68(1):207–214. https://doi.org/10.1080/11250000109356410

Carpaneto GM, Fattorini S. 2003. Seasonal occurrence and habitat distribution of tenebrionid beetles inhabiting a Mediterranean coastal dune (Circeo National Park, Italy). Revue d'Écologie (La Terre et La Vie) 58(3):293–306. https://doi.org/10.3406/revec.2003.5330. https://hal.science/hal-03529970

Cartagena MC, Galante E. 1999. Ecología de Tentyria laevis solier, 1835 y *T. peiroleri* Solier, 1835 (Coleoptera, Tenebrionidae, Tentyriini). Ses. Entom. ICHN-SCL 11(1):25–34. https://raco.cat/index.php/SessioEnto/article/view/192154

Cartagena MC, Galante E. 2003. Ecología del género Blaps Fabricius 1775 en el sudeste ibérico (Col. Tenebrionidae). Ses. Entom. ICHN-SCL 12(1):43–53.

Cheli CH, Carrara R, Banderi L, et al. 2021. Distribution and environmental determinants of darkling beetles assemblages (Coleoptera: Tenebrionidae) in Península Valdés (Argentinean Patagonia). An. Acad. Bras. Cienc. 93(3):e20201282. https://doi.org/10.1590/0001-3765202120201282

Di Stefano G, Fattorini S. 2000. Corologia italiana di Erodius siculus ed osservazioni eco-etologiche nel Lazio (Coleoptera: Tenebrionidae). Boll. Assoc. Romana Entomol. 55(2000):27–43.

Draney ML. 1993. The subelytral cavity of desert tenebrionids. Fla. Entomol. 76(4):539–549. https://doi.org/10.2307/3495783

Eisenhauer N, Bonn A, Guerra C. 2019. Recognizing the quiet extinction of invertebrates. Nat. Commun. 10(1):50. https://doi.org/10.1038/s41467-018-07916-1

Fallaci M, Colombini I, Chelazzi L. 1994. An analysis of the Coleoptera living along a Tyrrhenian beach-dune system: abundance, zonation, and ecological indices. Vie Milieu 44(1):243–256. https://hal.sorbonne-universite.fr/hal-03048050

Fattorini S. 2008. Ecology and conservation of tenebrionid beetles in Mediterranean coastal areas. In: Fattorini S., editor. Insect ecology and conservation. Trivandrum, Kerala: Research Signpost;p. 165–297.

Fattorini S. 2023. Adaptations of tenebrionid beetles to Mediterranean sand dune environments and the impact of climate change (Coleoptera: Tenebrionidae). Frag. Entomol. 55(1):1–20. https://doi.org/10.13133/2284-4880/1496

Fattorini S, Carpaneto GM. 2001. Tenebrionid density in Mediotyrrhenian coastal dunes: habitat and temporal variations (Coleoptera: Tenebrionidae). Frag. Entomol. 33(1):97–118.

Fernández JA. Guía de campo del Parque Nacional de Doñana. Barcelona (Spain): Omega Editions; 1982. p. 484.

García-Canseco V. Parque Nacional de Doñana. España: Canseco Editores, S.L. Talavera de la Reina; 2002.. p. 432.

García-Novo F, Marín-Cabrera C. Doñana: Water and Biosphere, Doñana. 2005 Project. Madrid: Guadalquivir Hydrologic Basin Authority, Spanish Ministry of the Environment; 2006. p. 365. https://unesdoc.unesco.org/ark:/48223/pf0000151554.locale=es

Hansen MC, Potapov PV, Moore R, et al. 2013. High-resolution global maps of 21st-century forest cover change. Science 342(6160):850–853. https://doi.org/10.1126/science.1244693

Harrison XA, Donaldson L, Correa-Cano ME, et al. 2018. A brief introduction to mixed effects modelling and multi-model inference in ecology. PeerJ 6(1):e4794.

Heatwole H, Harrington S. 1989. Heat tolerance of some ants and beetles from the pre-Saharan steppe of Tunisia. J. Arid Environ. 16(1):69–77. https://doi.org/10.1016/s0140-1963(18)31048-6

Hohbein R, Conway C. 2018. Pitfall traps: a review of methods for estimating arthropod abundance: pitfall traps: estimating arthropod abundance. Wild. Soc. Bull. 42(4):597–606. https://doi.org/10.1002/wsb.928

Karger DN, Conrad O, Böhner J, et al. 2017. Climatologies at high resolution for the earth's land surface areas. Sci. Data 4(1):1–20. https://doi.org/10.1038/sdata.2017.122

Kearney MR, Porter WP. 2020. Niche MapR – an R package for biophysical modelling: the ectotherm and dynamic energy budget models. Ecography 43(1):85–96. https://doi.org/10.1111/ecog.04680

Kellermann V, Overgaard J, Hoffman AA, et al. 2012. Upper thermal limits of *Drosophila* are linked to species distributions and strongly constrained phylogenetically. Proc. Natl. Acad. Sci. USA 109(1):16228–16233. https://doi.org/10.1073/pnas.1207553109

Khaliq I, Shahid MJ, Kamran H, et al. 2023. The role of thermal tolerance in determining elevational distributions of four arthropod taxa in mountain ranges of southern Asia. J. Anim. Ecol. 92(10):2052–2066. https://doi.org/10.1111/1365-2656.13996

Lahondère C. 2023. Recent advances in insect thermoregulation. J. Exp. Biol. 226(18):jeb245751. https://doi.org/10.1242/jeb.245751

Leo P, Manci C, Drăghici CA. The genus Tentyria Latreille, 1802 in Romania, with first record of *T. frivaldskii* Kraatz, 1865 (Coleoptera: Tenebrionidae). Cluj-Napoca: XXVIII-lea Simpozion Național de Entomologie al Societății Lepidopterologice Romine; 2018.

Leong CM, Tsang TPN, Guénard B. 2020. Critical Thermal maximum measurements and its biological relevance: the case of ants. BioRxiv 1(1):1–12. https://doi.org/10.1101/2020.12.09.417410

Lima C, Helene AF, Camacho A. 2021. Leaf-cutting ants' critical and voluntary thermal limits show complex responses to size, heating rates, hydration level, and humidity. J. Comp. Physiol. 192(2):235–245. https://doi.org/10.1007/s00360-021-01413-6

Liu JL, Liu CA, Li FR, et al. 2012. Influences of shrub vegetation on distribution and diversity of a ground beetle community in a Gobi Desert ecosystem. Biodivers. Conserv. 21(1):2601–2619. https://doi.org/10.1007/s10531-012-0320-4

Liu T, Liu H, Wang Y, et al. 2023. Climate change impacts on the potential distribution pattern of Osphya (Coleoptera: Melandryidae), an old but small beetle group distributed in the Northern Hemisphere. Insects 14(5):476. https://doi.org/10.3390/insects14050476

López-Sánchez S, de los Santos A, Montes C. 1985. Estudio de la forma larvaria de *Tentyria platyceps* Stev. 1829 (Col., Tenebrionidae). Eos 61(1):173–182. http://hdl.handle.net/10261/170594

Martín C, Seva E. 1990. Ciclos estacionales de actividad y modelos espaciales en las poblaciones de Coleoptera Tenebrionidae de las dunas costeras de la playa de El Saladar (Alicante-Elche, SE. de España). Mediterránea Ser. Biol. 12:97–112.http://dx.doi.org/10.14198/MDTRRA1990.12.08

Martín-López B, García-Llorente M, Palomo I, et al. 2011. The conservation against development paradigm in protected areas: valuation of ecosystem services in the Doñana social–ecological system (southwestern Spain). Ecol. Econ. 70(8):1481–1491. https://doi.org/10.1016/j.ecolecon.2011.03.009

Matthews EG, Lawrence JF, Bouchard P, et al. 2010. Tenebrionidae Latreille, 1802. In: Beutel RG, Leschen RAB, Lawrence JF, editors. Handbook of Zoology. A natural history of the phyla of the animal kingdom, IV Arthropoda: Insecta. Part 38. Berlin: Walter de Gruyter.p. 574–659

Montes C, Borja F, Bravo MA, Moreira JM. Reconocimiento biofísico de espacios naturales protegidos. Doñana: una aproximación ecosistémica. Bio-physical reconnaissance of protected áreas, Doñana: an ecosystem approach. Seville, Spain: Junta de Andalucía, Consejería de Medio Ambiente; 1998. p. 526.

Ojeda J, Vallejo I, Malvarez GC. 2005. Morphometric evolution of the active dunes system of the Doñana National Park, Southern Spain (1977–1999). J. Coast. Res. 49(1):40–45. https://www.jstor.org/stable/25737402

R Core Team. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing; 2020. https://www.r-project.org/

Rajpurohit S, Parkash R, Singh S, et al. 2008. Climate change, boundary increase and elongation of a pre-existing cline: a case study in *Drosophila ananassae*. Entomol. Res. 38(4):268–275. https://doi.org/10.1111/j.1748-5967.2008.00186.x

Rivas-Martínez S, Costa M, Castroviejo S, et al. 1980. Vegetación de Doñana (Huelva, España). Lazaroa 2(1):5–190.

Salado R. 1998. Coleópteros de los arenales costeros gaditanos. Importancia y protección de los hábitats. Rev. Soc. Gaditana de Hist. Nat 1(1):39–45.

Sánchez-Guillén R, Córdoba-Aguilar A, Hansson B, et al. 2016. Evolutionary consequences of climate-induced range shifts in insects. Biol. Rev. 91(1):1050–1064. https://doi.org/10.1111/brv.12204

Sánchez-Piñero F, Gómez JM. 1995. Use of ant-nest debris by darkling beetles and other arthropod species in an arid system in south Europe. J. Arid Environ. 31(1):91–104. https://doi.org/10.1006/jare.1995.0052

Sandall E, Maureaud AE, Guralnick R, et al. 2023. A globally integrated structure of taxonomy to support biodiversity science and conservation. Trends Ecol. Evol. 38(12):1143–1153. https://doi.org/10.1016/j.tree.2023.08.004

de los Santos A. 1992. Análisis de la estructura de la comunidad de Tenebrionidos en dos ecosistemas del bajo Guadalquivir (S.O. ESPAÑA): Factores ecológicos e históricos. Bol. Soc. Port. Entomol. 3(1):59–68.

de los Santos A, Montes C, Ramírez-Diez L. 1982. Modelos espaciales de algunas poblaciones de coleópteros terrestres en dos ecosistemas del bajo Guadalquivir. Mediterranea, Ser. Bio 6(1):65–92.

de los Santos A, Montes C, Ramírez-Diez L. 1988. Life histories of some darkling beetles (Coleoptera: Tenebrionidae) in two Mediterranean ecosystems in the lower Guadalquivir (Southwest Spain). Environ. Entomol. 17(5):799–814. https://doi.org/10.1093/ee/17.5.799

Suso J, Llamas MR. 1993. Influence of groundwater development on the Doñana National Park ecosystems (Spain). J. Hydrol. 141(1-4):239–269. https://doi.org/10.1016/0022-1694(93)90052-b

Taylor LR. 1984. Assessing and interpreting the spatial distributions of insect populations. Annu. Rev. Entomol. 29(1):321–357. https://doi.org/10.1146/annurev.en.29.010184.001541

Terblanche JS, Deere JA, Clusella-Trullas S, et al. 2007. Critical thermal limits depend on methodological context. Proc. Biol. Sci. 274(1628):2935–2942. https://doi.org/10.1098/rspb.2007.0985

Terblanche JS, Hoffmann AA, Mitchell KA, et al. 2011. Ecologically relevant measures of tolerance to potentially lethal temperatures. J. Exp. Biol. 214(Pt 22):3713–3725. https://doi.org/10.1242/jeb.061283

Vrieze SI. 2012. Model selection and psychological theory: a discussion of the differences between the Akaike information criterion (AIC) and the Bayesian information criterion (BIC). Psychol. Methods 17(2):228–243. https://doi.org/10.1037/a0027127

Werner, M. 2001. Shuttle radar topography mission (SRTM) mission overview. Frequenz. 55(3–4):75–79. https://doi.org/10.1515/FREQ.2001.55.3-4.75