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Landscape correlates of sand racer species (Lacertidae; *Psammodromus*) segregation in their contact area along the Conquense Drove Road (Cuenca, Iberian Peninsula)

Juan E. Malo[1,2,*], Antonio Martín-Higuera[3], Cristina Mata[1,2], Francisco M. Azcárate[1,2]

[1] Terrestrial Ecology Group (TEG-UAM), Departamento de Ecología, Facultad de Ciencias, Universidad Autónoma de Madrid, C Darwin 2, 28049 Madrid, Spain
[2] Centro de Investigación en Biodiversidad y Cambio Global (CIBC-UAM), Universidad Autónoma de Madrid, C Darwin 2, 28049 Madrid, Spain
[3] Área de Herpetología, Asociación Iberozoa, 28760 Tres Cantos, Spain

*Correspondence: je.malo@uam.es

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The Edwards's sand racer *(Psammodromus edwarsianus)* was recognised as distinct from the Spanish sand racer (*P. hispanicus)* a decade ago, but both their distributions and interspecific range limits are poorly defined. Results of sampling both species along 70km of the Conquense Drove Road (Central Spain) indicate a clear North/South segregation, with *P. edwarsianus* inhabiting the area North of Las Pedroñeras and *P. hispanicus* the South. The segregation corresponds with lithological and vegetation differences, hard calcareous substrates in the North and softer sandy sedimentary material in the South. The latter is associated with more intensive agricultural land-use in contrast to the persistence of copses and scrub on the calcareous terrain. The results provide new data on the regional distribution of both species. They also highlight the potential value of this species-pair as a model for study of interactions and habitat segregation in lacertids.

Key words: Allopatry; cañada; differentiation; distribution; niche; *Psammodromus edwarsianus*; *Psammodromus hispanicus*.

Comprehensive knowledge of taxonomy and species distribution is key to their conservation, given that it enables a focus on particular species and sites as well as on the most effective interventions (Groves *et al.* 2002, Mace 2004). Regarding reptiles, knowledge about distributions, even within Europe, is still fragmentary for many elusive species and further complicated by recent taxonomic revisions based on molecular analyses that have resulted in significant changes to the species list (Speybroeck *et al.* 2020). Identifying species distributions and the factors related to them is thus a priority in the continent, which is subject to intense anthropic pressures and climate change (Falaschi *et al.* 2019).

The Iberian Peninsula is an important region at the European scale for lacertid diversity, with 8 genera and 27 native species (García-Porta *et al.* 2019, Speybroeck *et al.* 2020). This diversity arises both from the confluence of taxa of Mediterranean and Atlantic affinities and the strong processes of evolutionary divergence of lacer-

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tids and other reptile groups recorded in the south-east and on both sides of the Strait of Gibraltar (KALIONTZOPOULOU *et al.* 2011, MARTÍNEZ-FREIRÍA *et al.* 2020). Recent taxonomic revisions of lacertids have resulted in the recognition of new Iberian species of the genera *Podarcis*, *Psammodromus* and *Timon* (SPEYBROECK *et al.* 2020). Nevertheless, information on the distribution of these species is very incomplete, even at a 10km-square scale (SIARE 2022), and their actual distribution ranges are conditioned by recent taxonomic changes, such as species-splitting. Investigating species distributions across contact zones between phylogenetically sister or cryptic species of the above genera is thus of outstanding relevance.

Sand racers of the *Psammodromus hispanicus* group constitute a paradigm in this respect. Three species have recently been recognised as independent entities according to morphological, genetic and ecological data (FITZE *et al.* 2011, SAN-JOSÉ *et al.* 2012): *P. occidentalis* inhabits western Spain and Portugal, *P. hispanicus* occupies a central belt in Spain and the known distribution of *P. edwarsianus* extends from south-east Spain along the Mediterranean coastlands as far as southwestern France, as well as large areas of inland Spain (BISBAL-CHINESTA & GARCIA-MARSÀ 2015, FARIA *et al.* 2021). Two species are thus endemic to the Iberian Peninsula but the range limits of all three are still poorly defined and suggest large areas of potential overlap. Phenotypic differences between *P. occidentalis* and *P. hispanicus* are small and they are thus difficult to separate in the field (FITZE *et al.* 2011). Therefore, uncertainty regarding their distribution limits, and the factors that underlie these, may persist for some time yet. In contrast, *P. edwarsianus* can be readily identified by the presence of a supralabial scale below the subocular scale (FITZE *et al.* 2011, SAN-JOSÉ *et al.* 2012), enabling its distribution relative to that of *P. hispanicus* to be clearly established within the vast expanse of potential range contact suggested by the most up to date information on their ranges (FARIA *et al.* 2021, SIARE 2022).

Consequently, these latter two Iberian sand racer species may conform an interesting model to study spatial patterns of overlap and segregation in phylogenetically close species (GOMES *et al.* 2016, CORDERO *et al.* 2021). Divergence of these species is dated around 4.78 (1.5–8.7) Mya, coinciding with the profound geographical and climatological changes that followed the opening of the Strait of Gibraltar after the Messinian salinity crisis (FITZE *et al.* 2011). Distribution models of both species at the Iberian Peninsula scale point to *P. edwarsianus* inhabiting drier, warmer areas with less shrub cover (FITZE *et al.* 2011), although such predictions may well differ at smaller spatial scales (BRAMBILLA *et al.* 2019, GOUDARZI *et al.* 2021). Both species have extensive ranges and are associated with grasslands having some degree of shrub cover, that therefore may be analysed along extensive, relatively continuous gradients that may respond quite rapidly to environmental changes.

Drove roads (termed *'Cañadas'* in Spanish), the traditional tracks used to move livestock between villages and grazing areas, have attracted scientific attention since they function as ecological corridors or wildlife reservoirs across highly dis-

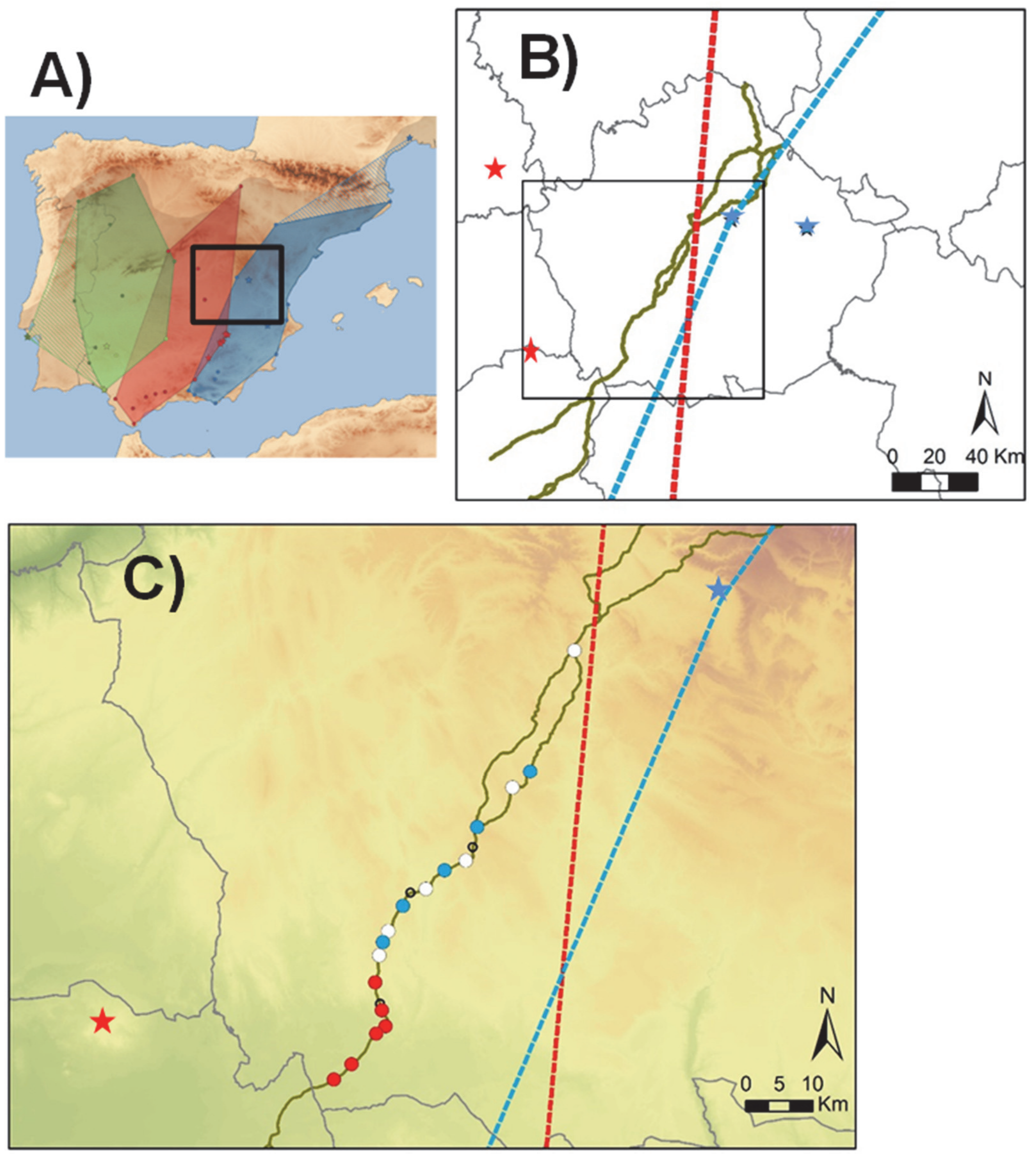

Figure 1: Spatial arrangement of sampling in relation to the known distribution of *Psammodromus hispanicus* (red) and *P. edwarsianus* (blue) according to Faria *et al.* 2021 (Map A). The black rectangle in map in A) is enlarged in B) to show in greater detail the two known localities of each species (red and blue stars, respectively) together with their distribution limits in the region (*P. hipanicus* to the west of red broken line, *P. edwarsianus* east of blue broken line), as well as the Conquense Drove Road in green. Thin black lines correspond to province limits. C) Locations of sampling points along the drove road with confirmed presence of *P. hispanicus* (red dots) and *P. edwarsianus* (blue dots) during this study. White dots correspond to locations with confirmed presence of sand racers where no capture was achieved, and empty circles show where no sand racers were observed. Red and blue lines and stars same as in B).

turbed landscapes (AZCÁRATE *et al.* 2013a, HILTY *et al.* 2020, MALO & MATA 2021). They are continuous strips of land, 20–75m wide, cutting across the whole territory, which were preserved for livestock movements and have remained unploughed since remote times. They have thus preserved ancient grasslands and their integral ecological processes (e.g., MANZANO & MALO 2006) and may serve as refuges for invertebrates or small vertebrates alike (AZCÁRATE *et al.* 2013b, HEVIA *et al.* 2013, 2016). In areas such as La Mancha (Central Spain), where most of the countryside is cropped, they are one of the few areas protected from ploughing and that may interconnect surviving small patches of natural grasslands, forests and scrub. The *'Cañada Real Conquense'* is outstanding in this respect since it connects the protected woodlands of the Sierra Morena with the Serranía de Cuenca, cutting across over 200km of the plains of La Mancha in the Provinces of Ciudad Real and Cuenca (OTEROS-ROZAS *et al.* 2013); one of the areas of the Iberian Peninsula known to have least connectivity for wildlife (RODRÍGUEZ *et al.* 2018). This drove road was thus selected for study since it has the potential to act as a refuge for sand racers, and it could be a good location for extending knowledge of sand racer distributions in their area of contact and for analysing the factors underlying the species limits between *P. hispanicus* and *P. edwarsianus*. In addition, it is one of the areas where the distribution limits between both species are least known (BISBAL-CHINESTA & GARCIA-MARSÀ 2015, FARIA *et al.* 2021).

This study relies on the morphological differentiation of *P. hispanicus* and *P. edwarsianus* to improve the knowledge on their distributions (MOLINA *et al.* 2020, FARIA *et al.* 2021). Specifically, the main aims of this study are (i) to determine the spatial distribution of *P. hispanicus* and *P. edwarsianus* along the Cañada Real Conquense in the Cuenca province, from the sierra foothills across to the cultivated plains, and (ii) to identify the spatial patterns of overlap and/or segregation for both species at the local scale. Finally, we aim to characterise the landscape of the study area (lithology, vegetation) and (iii) determine its influence on species distributional patterns.

MATERIALS AND METHODS

Study area

The study was carried out along a 70km sector of the Cañada Real Conquense, between Fresneda de Altarejos and Las Pedroñeras (Cuenca Province, Figure 1). This corresponds to a known area of contact between *P. hispanicus* and *P. edwarsianus* where no records attributed to each species exist (FARIA *et al.* 2021). This stretch spans a landscape and land use gradient from the foothills of the Sierra de Cuenca, with their abundant forest patches and little anthropic influence, to the intensively cultivated valley floor, where practically no unploughed terrain exists away from the drove road itself. These changes in terrain and land use accompany a change in lithology (Table 1, IGME 1985), with hard substrata of Cretaceous origin (limestones, dolomites and sandstones) predominating in the sierra and softer, sedimentary Neogene and Quaternary material (sand and silty soils,

Table 1: Geochronology of main lithologies present in the study area according to IGME (1985).

Geological Era / System	Lithology
Cenozoic / Quaternary	Gravels, conglomerates, sands and silts
Cenozoic / Miocene – Pliocene	Sandstones, conglomerates, clays, limestones and evaporites
Cenozoic / Paleogene – Neogene	Conglomerates, sandstones, clays, limestones and evaporites
Mesozoic / Cretacic	Dolomites, limestones, marl and sandstones
Mesozoic / Jurasic – Cretacic	Limestones, dolomites, marl, sandstones and conglomerates

conglomerates) in the valley bottom. The drove road here is well preserved, having continuous cover of grassland and scrub with scattered trees, only small areas having been tilled or otherwise modified.

Sampling

The area was first prospected in July 2020 when reptiles were searched for 20 minutes along each of the 13 transects and sand racer presence was confirmed along the length of the drove road. In April 2021, under optimum sampling conditions (12–18ºC temperatures and high reptile activity), 20 points of the drove road, including the original 13, were sampled. These were evenly spaced along the drove road (Average ± SD intersample distances 3329 ± 3890m, Figure 1). Two fieldworkers conducted an intensive search for sand racers along a transect at each sample point, checking habitat features regularly used by lizards, such as stone piles, walls and scrub patches, as well as looking under stones and other objects under which they might shelter. The transects spanned 500m along the drove road, centred on it and extending to either side to include its entire breadth (20–40m at most sites). Each transect was searched for 40 minutes. On transects where sand racers were present, all observed sand racers were annotated and attempts were made to capture up to three individuals to examine for the presence (*P. edwarsianus*) or absence (*P. hispanicus*) of a supralabial scale below the subocular scale (FITZE *et al.* 2011, SAN-JOSÉ *et al.* 2012). All captives were released unharmed where they were found, after identification.

Habitat characterization

The area occupied by different substrate types, associated with distinct geological periods (see Table 1), was measured, as well as the different extents of plant cover (woodland, scrub, grassland, crops), in order to investigate for environmental factors that might determine the segregation of the two species. These data were obtained for a 500m buffer zone centred on the midpoint of each transect employing a GIS. All spatial analyses were performed using geoprocessing tools under ArcGIS for Desktop 10.7 (Environmental Systems Research Institute, Redlands, CA) and official cartographies of lithology (IGME 1985) and vegetation from the CLC 2018 dataset in the CORINE landcover project (EEA, 2022).

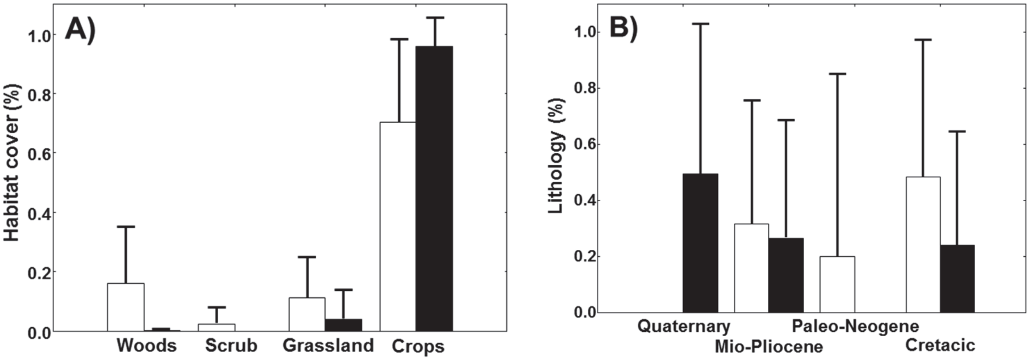

Figure 2: Average cover (+SD) of vegetation (left panel, A) and lithology (right panel, B) on transects with observations of *Psammodromus edwarsianus* (empty bars) and *P. hispanicus* (filled bars) along a section of the Conquense Drove Road.

The small altitudinal range of the study area (685–991m a.s.l.) relative to that known for the two species, and its limited spatial extent, precludes the occurrence of significant differences in large-scale climatic factors, such as those analysed by FITZE *et al.* (2011).

Statistical analyses

The GIS data obtained were converted to percentage cover and examined by non-parametric statistical analysis, given the low number of available observations. Spearman's r correlations were employed to assess relationships detected between lithographic and vegetational variables, while Mann-Whitney U tests were used to compare different cover values between observations for each species. The analyses were carried out with STATISTICA 8.0 (STATSOFT, 2007).

RESULTS

The April 2021 sampling found 57 sand racers in total on 17 of the 20 transects. Captures were successful on 11 transects, the species captured being *P. edwarsianus* (8 individuals) on five transects and *P. hispanicus* (13 individuals) on six transects. In seven transects we captured more than one sand racer, but there were no instances where both species were caught on the same transect. As evident in Figure 1C, all *P. edwarsianus* observations were in the northern part of the sampled area, at altitudes of 856–911m a.s.l., and those of *P. hispanicus* were in the south, at 685–750m. a.s.l. The transects that marked the confirmed separation of the two species were 6.14km apart, including in the middle one transect where no individuals could be captured.

For the 11 transects where lizards were captured taken together, the increase in crop cover correlates with reduced woodland (R = -0.81; $p = 0.002$), scrub (R = -068; $p = 0.022$) and grassland (R = -0.88; $p < 0.001$) cover; and the cover of grasslands is associated with those of woodlands (R = 0.68; $p = 0.021$) and scrub (R = 0.77; $p = 0.006$). Moreover, there is a positive association between Cretaceous substrate cover and grasslands (R = 0.091; $p < 0.001$) and a negative association between such substrate and cultivation (R = -0.85; $p = 0.001$). However, at the scale of buffers the extent of different lithologies shows no correlation with each other ($p > 0.1$ in all cases).

The observations of both species show differences between them with respect to lithology and vegetation (Figure 2), although the small sample sizes and the variability present within the buffer zones restricts the clarity of the results. Nevertheless, there is a significant association of *P. hispanicus* with high cover values of Quaternary substrates (adjusted Z = -2.12, $p = 0.034$); and a marginal tendency of *P. edwarsianus* to occur in areas of greater tree cover (adjusted Z = 1.69; $p = 0.091$).

DISCUSSION

The results provide detailed information on the distribution of the two species in a previously poorly defined contact area and they point to a spatial pattern of no overlap, likely mediated by distinct habitat selection. These last data may be useful in refining species distribution models at small spatial scales, such as it has been the case with various taxonomic groups (BRAMBILLA *et al.* 2019, GOUDARZI *et al.* 2021). They also offer the possibility of using Iberian sand racers as model species for studying niche segregation (ROUAG *et al.* 2007, FASOLA *et al.* 2020).

Our data supply an initial but rather detailed definition of the distribution limits of the two species in central Cuenca province, though a more intense survey could refine it at a more local scale. To be specific, our observations indicate a North/South segregation here, such that *P. edwarsianus* detections happened from the sierras to north of Las Pedroñeras, while *P. hispanicus* occurs further south from there. This amounts to a small westward extension of the previously known inter-specific boundary that was based on genetic analysis of a few individuals (FARIA *et al.* 2021, Figure 1). Thus five 10-km UTM squares (WK50, WJ49, WJ48, WJ38, WJ37) are added to the known Iberian distribution of *P. edwarsianus* (SIARE 2022). There are existing records of *P. hispanicus* from two of them (WJ49 and WJ38) although both may date from before the species were split. Our captures show that one of the new squares (WJ37) is shared by *P. hispanicus* and *P. edwarsianus* and they also add one new square (WJ25) to the known range of *P. hispanicus*. It is emphasised that all the sampled sites form part of the continuous strip that is the Cañada Real Conquense or "de los Chorros" drove road and that there are no obstacles to species dispersal along it. The morphological differences that allow in-the-hand differentiation of the two species will facilitate intensive studies of their distribution and ecology (SAN-JOSÉ *et al.* 2012, MOLINA *et al.* 2020), which will not only permit the inter-species boundaries to be mapped rapidly but also will allow these lacertids to serve as a model for studying segregation by habitat among sister species. Such studies at fine scales will require the complementary use of genetic tools (e.g., microsatellites) to assess potential gene flow between species in their contact zone, as it occurs in other reptiles (CARRETERO 2008, SPEYBROECK *et al.* 2020).

Our results suggest that the two species are segregated on a landscape scale (in the range of one to a few kilometres) as a function of substrate type and land use. In the study area, substrate type has historically conditioned human use and restricted cropping to softer and deeper soils, and the relevance for sand racer distributions of lithology and vegetation structure can thus not be disentangled. *Psammodromus edwarsianus* is associated with harder substrates of non-Quaternary origin subject to less human impact and offering habitat mosaics with copses, scrub and patches of permanent grassland. In contrast, *P. hispanicus* occupies more modified areas; croplands with patches of grassland on softer substrata (see however BISBAL-CHINESTA & GARCIA-MARSÀ 2015). There is an altitudinal difference between the capture sites of the two species but in view of the wider distribution of both, and since *P. edwarsianus* inhabits low altitude sites throughout its Mediterranean distribution (FITZE *et al.* 2011, FARIA *et al.* 2021), this may just indicate local co-variation with substrate types and vegetation. Their separation according to landscape factors refines previous eco-evolutionary descriptions regarding the species limits on a regional scale, rooted in their evolutionary divergence around the Miocene-Pliocene transition and reflected at present on the more pronounced Mediterranean macroclimate of the eastern area occupied by *P. edwarsianus* (greater seasonality of precipitations, higher temperatures during the wettest quarter and milder winters; see FITZE *et al.* 2011).

Within the framework of a hierarchical habitat selection of species (MORIN *et al.* 2020), such differentiation at the geographical scale defines the broad East/West segregation of the two species. Meanwhile factors linked to lithology and landscape structure correspond with the North/South segregation detected in our study area at a kilometric scale. There may possibly also be some fine-scale differentiation of habitat selection between the two species involving competition and/or some other distinct community context, which would merit closer investigation. At this scale, very local variables related to microclimate, plant cover, productivity and refuge should be also included to fully understand the underlying variables responsible of segregation, which could be also linked to morphological variables of the species (BOMBI *et al.* 2009, GOMES *et al.* 2016). The small morphological differences between the two species (FITZE *et al.* 2011, SAN-JOSÉ *et al.* 2012) may be significant in this regard: in particular, *P. hispanicus* is somewhat larger and heavier with a broader head whereas *P. edwarsianus* is slender and proportionately longer-tailed. Alongside this, the plant communities of the limestone and other hard substrates where *P. edwarsianus* was found largely consist of permanent grassland and dwarf scrub, whereas annual grasses and bare ground predominate on the drier, sandier substrates occupied by *P. hispanicus* (MATEO SANZ 1996). Such vegetational differences have been found elsewhere to be important for lacertid segregation (MIZSEI *et al.* 2020), although other features such as differences in aggressiveness may also be involved in interspecific segregation at local scales (VANHOOYDONCK *et al.* 2000, DOWNES & BAUWENS 2002).

Finally, this study offers a new perspective on the processes that underlie spatial segregation between sand racer species, and it suggests interesting avenues for further investigation. In the first instance, it would be useful to replicate this type of sampling at other locations where *P. hispanicus* and *P. edwarsianus* meet, in order to refine distribution maps and to confirm the significance of landscape variables that may determine species limits. A more intense survey of our study area could also refine the definition of range limits of the species there and confirm or not their local segregation described here, which is based on a small sample size. The value of a detailed study of competition/segregation between these two sister species at a spatial scale of a few tens of metres is also highlighted, given that our results suggest that there may exist sites of practically direct contact between individuals of both of them (ELSTROTT & IRSCHICK 2004, ROUAG *et al.* 2007, CARRETERO 2008, GOMES *et al.* 2016). The same situation would permit the existence of reproductive isolation based on phenotypic features between the two species to be investigated (GABIROT *et al.* 2012, SAN-JOSÉ *et al.* 2012). Drove roads would be outstandingly useful for such studies since these strips of land represent large experimental transects that cross landscapes, traversing all manner of substrate and vegetation types, serving as biological corridors for all organisms, particular small or medium-sized ones such as lacertids relying on grasslands (HILTY, *et al.* 2020).

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