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LEARNING FROM A MULTIDISCIPLINARY APPROACH:
THE EVOLUTION OF A WIDELY INTRODUCED
MEDITERRANEAN GECKO

SUMMARY

The Moorish gecko *Tarentola mauritanica* has a widespread circum-Mediterranean distribution. Because it is frequently associated with humanized infrastructures, accidental introductions into new areas have been reported, such as into most Mediterranean islands, Madeira, South America, the United States, and the Azores archipelago. Surprisingly, all introduced individuals belong to the same mitochondrial clade, known as the European clade, suggesting that the animals from this group are more prone to be introduced and also more successful in colonizing distinct environments. Following a multidisciplinary approach under genetic, ecophysiological and niche evolution frameworks, we intend to uncover the phenotypic attributes of this species that allows them to be such a successful colonizer. The lack of morphologically diagnosable characters typical of cryptic species poses a particular problem to taxonomists. Phylogenetic studies on the Moorish gecko uncovered extremely high levels of mtDNA diversity with six identified clades. Because of the conserved morphology of this species and lack of monophyly relative to *T. angustimentalis*, it has been suggested that *T. mauritanica* is a cryptic species complex that originated around 6 Mya. The recent addition of novel genetic markers and Bayesian coalescent species delimitation analysis support all six mitochondrial clades as “unconfirmed candidate species”, pending morphological data to define them. The quantification of realized niche overlap and the integration of species distribution models (SDMs) with calibrated phylogenies to study niche evolution are becoming powerful tools to understand speciation events. Our results suggest that diversification within *T. mauritanica* during the Miocene and Pleistocene is associated with both niche divergence and niche conservatism, related to temperature and humidity. Specifically, our ecophysiological experimental studies suggest that individuals from European populations display a trend for higher water loss, but higher variance compared with the Iberian populations. The detection of a phylogenetic signal suggests divergent evolutionary responses to the environment, which may account for the differences in their range expansion.

Key words. *Tarentola mauritanica*, introduced species, species delimitation, ecophysiology, niche evolution.

RIASSUNTO

Il Geco comune *Tarentola mauritanica* ha un'ampia distribuzione nell'area circum-Mediterranea. Specie antropofila, è soggetta a introduzioni accidentali, come è avvenuto nella maggior parte delle isole del Mediterraneo, a Madeira, in Sud America, negli Stati Uniti e nell'Arcipelago delle Azzorre. È sorprendente notare come tutti gli individui introdotti appartengano al medesimo clade, noto come clade europeo; ciò fa supporre che gli individui provenienti da questo gruppo siano più soggetti al trasporto e più efficaci nel colonizzare diversi tipi di ambiente. Attraverso un approccio multidisciplinare, che tenga conto di aspetti legati alla genetica, alla ecofisiologia e all'evoluzione delle nicchie, ci siamo proposti di indagare le caratteristiche fenotipiche che rendono la specie un efficiente colonizzatore. La mancanza di tratti morfologici rilevabili, tipici di specie criptiche, costituisce un ostacolo per i tassonomi. Gli studi filogenetici condotti sul Geco comune hanno evidenziato elevati livelli di diversità nel mtDNA, identificando sei distinti cladi. Tenendo conto della scarsa variabilità morfologica della specie e della mancanza di monofilia di *T. angustimentalis*, è stato ipotizzato che *T. mauritanica* possa essere un complesso di specie originatosi circa 6 Ma fa. La recente aggiunta di nuovi marcatori genetici e l'analisi bayesiana di delimitazione di specie coalescenti supportano i 6 cladi come "specie candidate non ancora confermate", in mancanza di dati morfologici per la loro definizione. La quantificazione della sovrapposizione delle nicchie realizzate e l'integrazione di modelli di distribuzione delle specie (Species Distribution Models, SDMs) con una filogenesi calibrata nello studio dell'evoluzione delle nicchie, stanno diventando strumenti sempre più potenti per comprendere gli eventi di speciazione. I nostri risultati suggeriscono che la differenziazione genetica di *T. mauritanica* durante il Miocene e il Pleistocene è associata sia a divergenza di nicchia sia a conservatorismo di nicchia, in relazione a temperatura e umidità. Nello specifico, i nostri studi sperimentali sulla ecofisiologia della specie indicano per gli individui provenienti da popolazioni europee una tendenza verso una maggiore perdita di acqua, ma anche una variabilità più elevata rispetto alle popolazioni iberiche. L'individuazione di un segnale filogenetico suggerisce risposte evolutive divergenti rispetto all'ambiente, fenomeno che può spiegare le differenze nell'espansione dell'areale.

Parole chiave. *Tarentola mauritanica*, specie introdotte, delimitazione delle specie, ecofisiologia, evoluzione della nicchia

The Moorish gecko *Tarentola mauritanica* is one of the most common geckos in the Western Mediterranean Basin, distributed across southern Europe (Iberian Peninsula, France, Italy, the Balkans, and Greece), North Africa (Morocco, Algeria, and Tunisia), and most of the Mediterranean islands (VOGRIN *et al.*, 2017). *Tarentola mauritanica* is known to be frequently associated with humanized environments, such as houses and stone walls, especially near artificial lights that attract insect prey (ARNOLD & OVENDEN, 2002). This close relationship with humans, frequently leads to accidental anthropogenic introductions of these geckos into new areas (ARNOLD & OVENDEN, 2002), such as the Balearic Islands and Tenerife (Spain), the islands of Madeira and Azores (Portugal), South America and the United States (VOGRIN *et al.*, 2017). Surprisingly, all individuals introduced into these new areas belong to the same mitochondrial genetic cluster (HARRIS *et al.*, 2004a, 2004b; RATO *et al.*, 2010, 2012, 2015b, 2016), suggesting not only

that these individuals seem more prone to be introduced, but also that they possess some phenotypic trait that allows them to be so successful. This is what we intend to reveal following a multidisciplinary approach focused on genetics, ecophysiology and niche evolution.

The lack of morphologically diagnosable characters typical of cryptic species poses a particular problem for taxonomists. This is especially true when taxa are closely related, sharing a high degree of ancestral polymorphism. Phylogenetic studies on the Moorish gecko species-complex *Tarentola mauritanica* uncovered extremely high levels of mtDNA diversity with six identified clades, including one from the Canary Islands identified as *T. angustimentalis* (RATO *et al.*, 2015a). Because of its conserved morphology and its paraphyletic status with respect to *T. angustimentalis*, it was suggested that *T. mauritanica* constitutes a cryptic species complex. Nevertheless, none of the nuclear loci used were reciprocally monophyletic regarding the mitochondrial lineages due to retention of ancestral polymorphism. In our study, we added three new intron markers to the already available dataset and used additional tools, namely phylogenetic gene trees, species tree and species limits within a Bayesian coalescent framework to confirm the support for the main lineages. Bayesian clustering analysis supports all six mtDNA lineages as independent groups, despite showing signs of ancestral polymorphism or possibly gene flow between the Maghreb/South Iberia and Central Morocco clades. The species tree recovered two major groups; one clustering taxa from Europe and Northern Maghreb and another one encompassing the lineages from Central/Southern Morocco, Central Morocco and the Canary Islands, indicating that the ancestor of *T. angustimentalis* came from the Central/Southern Morocco region. Finally, Bayesian coalescent species delimitation analysis supports all six mitochondrial clades as “unconfirmed candidate species”, pending morphological data to define them (RATO *et al.*, 2016).

The quantification of realized niche overlap and the integration of species distribution models (SDMs) with calibrated phylogenies to study niche evolution are not only powerful tools to understand speciation events, but can also be used as proxies regarding the delimitation of cryptic species. We applied these techniques in order to unravel how the fundamental niche evolved during cladogenesis within the *Tarentola mauritanica* species-complex. Our results suggest that diversification within this complex, during the Miocene and Pleistocene, is associated with both niche divergence and niche conservatism, with a pattern that varies depending on whether the variables involved are related to the seasonality or mean values of temperature and humidity. Moreover, climatic variables related to humidity and temperature seasonality were involved in the niche shift and genetic diversification of the

European/North African clade during the Pleistocene and in its maintenance in a fundamental niche distinct from that of the remaining members of the group (RATO *et al.*, 2015a). This study further highlights the need for a taxonomic revision of the *T. mauritanica* species-complex.

Because the fitness of ectotherms, including reptiles, is highly dependent on temperature and water availability, the study of ecophysiological traits, such as preferred temperature (T_p) and water loss rates (WLRs), may provide mechanistic evidence for the factors restricting the species ranges. In the Iberian Peninsula, two parapatric sister forms of the *T. mauritanica* complex, known as the Iberian and the European clades, are found. Ecological models previously performed using presence records and bioclimatic variables suggest niche divergence between the lineages is correlated with precipitation rather than with temperature (RATO *et al.*, 2015a). In this study, we test this correlative hypothesis using ecophysiological evidence. In the laboratory, we analyzed the T_p and WLRs for 84 adult males from seven distinct populations ascribed to one of the two lineages present in Iberia. Specifically, we evaluated the existence of trait conservatism versus adaptation among populations, lineages, or both. In addition, we tested for a trade-off between water and thermal traits and assessed whether climate regime of sampling localities had any influence on the ecophysiological patterns found. We found that T_p is quite conserved at both the population and lineage levels and independent from body size. In contrast, water loss experiments revealed some variation among populations, but the regression analysis failed to detect correlation between T_p and WLR at any level. Overall, the European lineage displayed a trend for higher water loss and greater diversity among populations when compared with the Iberian lineage. The lack of correspondence between ecophysiological traits and local climatic conditions favors phylogenetic signal versus adaptation. This suggests divergent evolutionary responses to the environment, mainly acting on water ecology in both lineages, which may account for the differences in their range expansion (RATO & CARRETERO, 2015).

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