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ORIGINAL ARTICLE

Lizards on the borders: source and patterns of colonization of an opportunistic reptile, *Podarcis siculus*, on the remote island of Pantelleria (Italy) depicted by mtDNA phylogeography and dorsal pattern

Carlotta Antinucci[1] · Francesco Gallozzi[1,2] · Leonardo Ancillotto[3,4] · Emiliano Mori[3,4] · Riccardo Castiglia[1,4]

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Abstract
Understanding patterns and modalities of species' colonization in insular ecosystems is a major goal of biogeography and may be key to decision makers, in terms of e.g., management and conservation. In this paper, we assess source and patterns of colonization of an opportunistic reptile, *Podarcis siculus*, on the remote island of Pantelleria (Italy), following a multidisciplinary approach combining molecular phylogeography and dorsal pattern analyses. We analyzed the mitochondrial gene cytochrome b (cytb) from 13 lizards and we assessed the frequency of the dorsal pattern phenotypes observing 188 basking lizards from eight localities throughout the island. The parsimony network revealed that haplotypes from Pantelleria belong to a haplogroup characteristic of western Sicily with the most common haplotype from Pantelleria being also found in three Sicilian localities. Unlike other Italian island populations, the dorsal pattern is highly conserved on Pantelleria, as a high percent of the observed individuals show the pattern also found in the hypothesized source area in western Sicily. In conclusion, our results are compatible with an allochthonous origin of the *P. siculus* population of Pantelleria Island. Thus, the species would need no population monitoring programme for its conservation on the island.

Keywords Biogeography · Invasion biology · Italian wall lizard · Mediterranean basin

Introduction

Understanding patterns and modalities of species colonization is a key goal of biogeography, particularly in insular ecosystems (Simberloff 1974; Helmus et al. 2014). Islands represent natural laboratories for the study of animal ecology, and the study of island biogeography claims a very long tradition, fascinating scientists since centuries (Whittaker et al. 2017). In such a context, the Mediterranean Basin offers a plenty of opportunities to test hypotheses and to verify patterns of island colonization, since it is one of the most archipelagos-rich basins in the Palearctic, besides representing a well-known biodiversity hotspot, and one of the areas with the longest history of human presence in the world (Blondel 2008). Nonetheless, biogeography knowledge of Mediterranean small islands is still relatively limited to few case studies and taxa, leaving wide space for deepening our understanding of ecological and biogeographical processes.

The rich network of traveling routes by both air and sea throughout the Mediterranean, for either commercial transport or tourism, is recognized as a key driver of species translocations across the area, with huge implications for biodiversity conservation and species management. As an example, several human-associated vertebrates such as commensal rodents (*Rattus* spp. and *Mus* spp.), birds (*Columba livia* var. *domestica*) and reptiles (e.g., *Tarentola*

Carlotta Antinucci and Francesco Gallozzi contributed equally to this work.

✉ Riccardo Castiglia
riccardo.castiglia@uniroma1.it

[1] Dipartimento di Biologia e Biotecnologie "Charles Darwin", Università di Roma "La Sapienza", Rome, Italy

[2] National Research Council, Research Institute on Terrestrial Ecosystems, Via Salaria km 29.300, Montelibretti, Rome I-00015, Italy

[3] CNR-IRET, Via Madonna del Piano 10, 50019 Sesto Fiorentino, Florence, Italy

[4] National Biodiversity Future Center, Palermo 90133, Italy

spp. geckoes) now widely occur in several islands, likely due to passive human transportation (Angelici et al. 2009; Ruffino and Vidal 2010; Goldberg et al. 2011; Phillips et al. 2012; Rato et al. 2012; Sciandra et al. 2022). In all such cases, understanding the origin of these species when found on islands may be key to decision makers, in terms of, e.g., management and conservation e.g., for deciding whether to monitor and conserve or not a taxon.

The Italian wall lizard, *Podarcis siculus* (Rafinesque-Schmaltz, 1810) (Squamata, Lacertidae) is a small-sized lizard that occurs in peninsular Italy, Sicily, Sardinia and Corsica, along the northern part of the eastern Adriatic coast as well as on several smaller islands and islets. The species is also found outside of its native range by having colonized several parts of the world due to human-mediated passive transport (Silva-Rocha et al. 2012, 2014; Kolbe et al. 2013; Oskyrko et al. 2022). The reason for this widespread diffusion is believed to be its great adaptability and competitiveness compared to other local lacertids (Kapsalas et al. 2016; Ribeiro and Sá-Sousa 2018). Its ability to colonize and establish stable populations even on tiny islands has made it one of the most widespread terrestrial vertebrate species in the Western Mediterranean countries.

The spatial genetic structure of this species in its native range is characterized by a mosaic of mitochondrial lineages, mostly parapatrics, whose origin dates back to Early-Middle Pleistocene, when a series of historical fragmentation events occurred with the onset of geographical barriers (Bonfiglio et al. 2002). Thus, six mtDNA clades have been found in peninsular Italy and Sicily (Senczuk et al. 2017) and, within each of them, different haplogroups have been identified, partially linked to distinct geographical regions (Senczuk et al. 2017). This spatially organized genetic structure has allowed to determine the source of many insular divergent populations, as well as populations located outside the native range (Silva-Rocha et al. 2012, 2014; Kolbe et al. 2013; Senczuk et al. 2018; Oskyrko et al. 2022). The Italian wall lizard also shows a remarkable polymorphism in the dorsal pattern (DP hereafter) which finds some correspondence with the genetic structure (Gallozzi et al. 2022).

Pantelleria is a volcanic island settled in the Sicilian Channel (Fig. 1), 100 km southwest of Sicily and 60 km east of the Tunisian coast. Its geographical position, halfway between Africa and Europe, makes it a very interesting location from a biogeographic point of view as its fauna has been shaped by colonization from both areas (e.g., Fichera et al. 2022; Sciandra et al. 2022). As to the herpetofauna on Pantelleria, five species are reported: *Hemidactylus turcicus* (Linnaeus, 1758), *Tarentola mauritanica* (Linnaeus, 1758), *Podarcis siculus*, *Chalcides ocellatus* (Forskål, 1775) and *Hemorrhois hippocrepis* (Linnaeus, 1758). Among those, *C. ocellatus* and *H. hippocrepis* have been the subjects of molecular genetic studies (Stöck et al. 2016; Faraone et al. 2020; Mori et al. 2022). For both species, a North African origin has been hypothesized which, however, appears to be very recent for *H. hippocrepis* and more ancient for *C. ocellatus* (Stöck et al. 2016; Faraone et al. 2020; Mori et al. 2022).

From a phenotypical point of view based on the DP, the Pantelleria population of *P. siculus* is believed to belong to

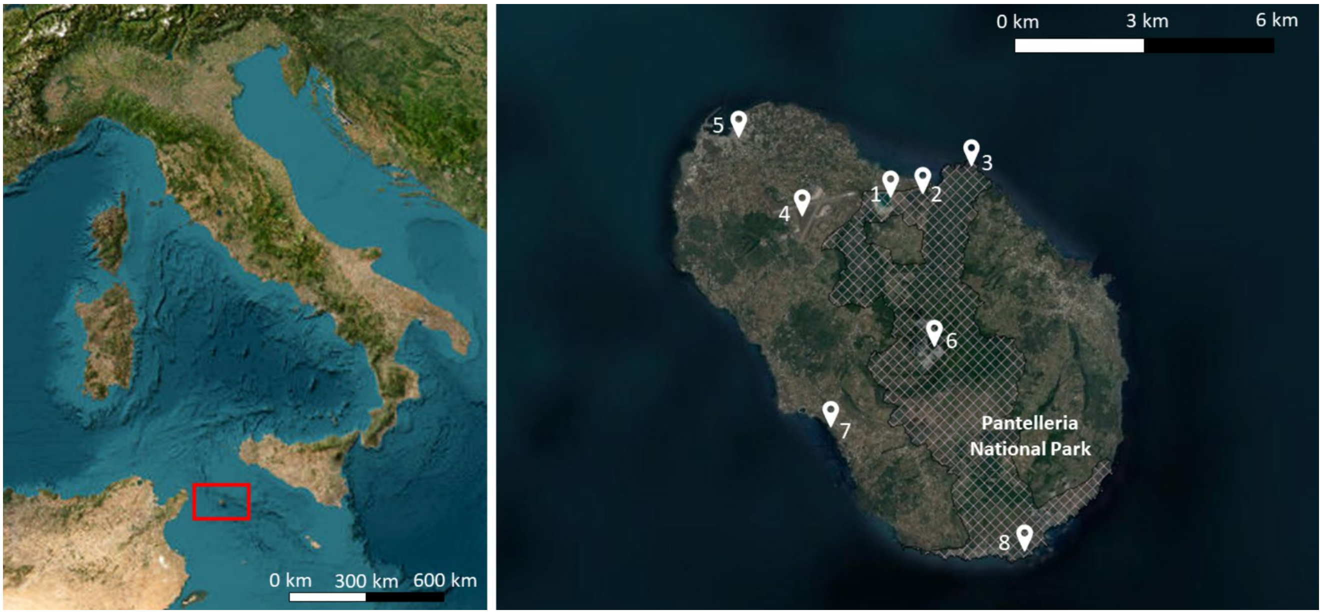

Fig. 1 Map of Pantelleria with sampling localities. The grid indicates the boundaries of the Pantelleria National Park. See Table 1 for localities details. Map from the open-source database of ISPRA (The Italian Institute for Environmental Protection and Research, http://sgi2.isprambiente.it/mapviewer/), modified by the authors

the nominal subspecies *P. s. siculus* (Rafinesque-Schmaltz, 1810), present in Sicily and southern Italy (Boulenger 1920–1921; Mertens 1926; Lanza 1973). A study based on allozymes (Capula 1994) suggested an anthropogenic origin of the Pantelleria population, yet from a low number of individuals from peninsular Italy.

In this paper we assess source and patterns of colonization of a remote island by an opportunistic reptile, using *P. siculus* on Pantelleria as a model, by following a multidisciplinary approach combining molecular phylogeography and dorsal pattern analysis.

Materials and methods

For genetic analysis, 13 lizards were collected by hand in May 2021 and in May and September 2022 from four localities within Pantelleria Island. Tissues were obtained from small tail tips by inducing autotomy after light pressure, all the individuals were released at the capture site (Fig. 2; Table 1). Tail tissues were stored in 96% pure ethanol. Genomic DNA was extracted from all the tissue samples by means of the universal extraction protocol (Aljanabi and Martinez 1997). We analyzed the mitochondrial gene cytochrome b (cytb). Amplification was carried

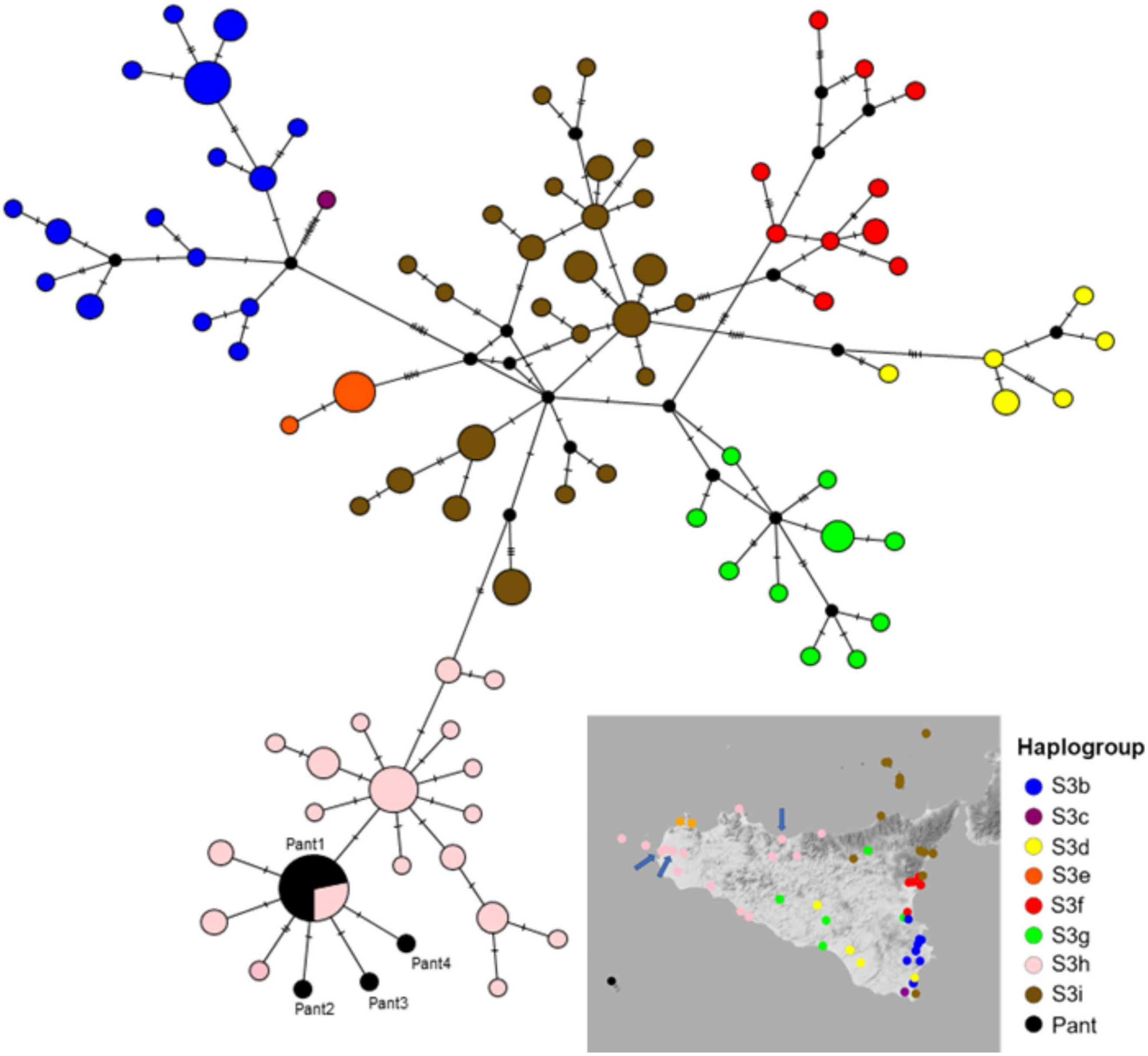

Fig. 2 Statistical parsimony network with the haplogroups from Sicily (S3 clade) and Pantelleria. The geographical distribution of the haplogroups of Sicily is shown in the map at the bottom right (modified from Senczuk et al. 2017). Specimens from Sicily sharing haplogroups with Pantelleria are indicated by arrows

Table 1 Number of analyzed/observed specimens for each of the localities shown in Fig. 1

Locality (N° on map)	Latitude	Longitude	cytb	Dorsal pattern
1 Bagno dell'Acqua	36.813	11.987	9	95
2 Strada perimetrale dietro Isola	36.815	12.013	1	7
3 Laghetto delle Ondine	36.825	12.005	-	18
4 Airport	36.813	11.963	1	7
5 Pantelleria (town)	36.831	11.943	-	20
6 Montagna Grande	36.781	12.005	2	12
7 Scauri	36.770	11.964	-	16
8 Salto la Vecchia	36.738	12.011	-	13

out using the primers employed by Podnar et al. (2005) Cyt F (5′-TTTGGATCACTATTRGGCCTCTGCC-3′) and H15425 (5′-GGTTTACAAGACCAGTGCTTT-3′) and using the following protocol: an initial denaturation at 94 °C for 2 min followed by 35 cycles with denaturation at 95 °C for 10 s, annealing at 55 °C for 20 s, and elongation at 72 °C for 90 s and a final extension at 72 °C for 7 min. Sequences were obtained using an external service (Macrogen).

The obtained cytb sequences (765 bp) were compared to the entire sequences database with the BLAST algorithm (https://blast.ncbi.nlm.nih.gov/Blast.cgi) using the newly obtained sequences and searching for highly similar sequences (Mega BLAST) in the entire nucleotide collection database. Based on the result of BLAST (see the results) it was possible to undoubtedly identify the clade which the haplotypes from Pantelleria belong to (clade S3) (Senczuk et al. 2017). Therefore, an alignment was made with 142 sequences belonging to the S3 clade (Genbank accession numbers KY064841-KY064982, Online resource: Table S1). Sequences of cytb were aligned with MUSCLE (Edgar, 2004) in MEGA (version 11.0.13; Tamura et al. 2021). Then a statistical parsimony (TCS) network was built using the software PopArt (version 1.7; Leigh and Bryant 2015) to visualize the relationships between haplotypes and infer about the origin of the Pantelleria haplotypes.

In order to assess the frequency of the dorsal pattern (DP) phenotypes we observed 188 basking lizards from eight localities across the entire islands (Figs. 2 and 3, and Table 1). The DP of each observed individual was evaluated and assigned to one of the five categories defined by Gallozzi et al. (2022), simply observing the specimens while they were basking or analyzing the pictures taken by camera.

Fig. 3 The two types of DP found in Pantelleria Island: reticulated, on the right, and the intermediate reticulated/campestris, on the left (pattern as defined in Gallozzi et al. 2022)

Results and discussion

In the 13 analyzed specimens from Pantelleria four different haplotypes (PANT1-4; GenBank accession numbers OR289688-OR289691) have been found. One of the haplotypes PANT1-4 is present in 10 individuals, while the other three are unique haplotypes that diverge from PANT1 for a single SNP. The analysis with the BLAST algorithm revealed that these four haplotypes show, at most, one point mutation compared to haplotypes from the S3 clade, a clade identified by Senczuk et al. (2017) in Sicily. Following this preliminary result, we decided to build a network using only the haplotypes deriving from the S3 clade. A map of the seven haplogroups belonging to the S3 clade in Sicily was drawn modifying the picture from Senczuk et al. (2017) to visualize the origin of Pantelleria's haplotypes with respect to different parts of Sicily (Fig. 2).

The topology of the statistical parsimony network revealed that the four haplotypes of Pantelleria belong to the haplogroup S3h (*sensu* Senczuk et al. 2017) characteristic of western Sicily (Fig. 2). Specifically, PANT1 is identical to a haplotype found in three localities settled in the northern part of the S3h range (arrows in map).

The occurrence of *P. siculus* on islands is potentially explained in several ways, including models of vicariance for continental islands and both ancient and recent dispersal events, in some cases mediated by human intervention as well (Senczuk et al. 2018; Buglione et al. 2019; Zuffi et al. 2022; Gallozzi et al. 2023). The fact that the most common haplotypes in Pantelleria are shared with some Sicilian localities suggests a single recent colonization event. On the other hand, the cytb gene is a mitochondrial locus which can give information only on female origins, because of its matrilinear genealogy. The alternative hypothesis that the island was colonized by the same haplotype several times and independently, appears unlikely considering the high haplotype diversity present in the source area (Sicily). This interpretation is compatible with the allozymic data of Capula (1994) who hypothesized a colonization of the island starting from a small number of individuals. However, in this previous study, the peninsular populations were assumed as the source area of the Pantelleria population, whereas our results show very clearly that the origin is from western Sicily. As far as the DP is concerned, it is highly conserved in all the animals observed in Pantelleria. Indeed, out of the total of 188 observed lizards, 180 presented a reticulated pattern and only 8 lizards showed an intermediate reticulated/campestris pattern (see Fig. 3). The reticulated pattern is also the most common one in the hypothesized source area in western Sicily (Gallozzi et al. 2022). Moreover, in the genus *Podarcis*, populations inhabiting the small islands of the Mediterranean are often characterized by a high chromatic polymorphism and this has been related to mixed ancestry of these populations (Yang et al. 2021). This can be extended to DP polymorphism found on islands in *Podarcis siculus* (Gallozzi et al. 2023). Therefore, the low diversity in the DP found in Pantelleria is compatible with the mtDNA results indicating a single introduction. This pattern is different from that found on other islands where a recent introduction has taken place such as in Gorgona Island (Tuscan Archipelago). In this case, Zuffi et al. (2022) assumed that colonization took place at least with three unrelated female founders from the mainland through distinct introductions.

The colonization times of the island cannot be evaluated considering the absence of differentiation between Pantelleria and the source area. However, it is possible to hypothesize a colonization that took place in historical times. As far as we know, the first report of the species in literature is found in a monograph from 1920 (Boulenger 1920). Even though *P. siculus* is not recorded in older studies, it could have been considered as a non-noteworthy species compared to the others living on the island (Doderlein 1881; Camerano 1891; Minà Palumbo 1893). Therefore, the colonization could even date back to the beginning of Roman settlements in 255 BC (Wilson 2021). Anyway, the high distance of the island from the coast tends to exclude natural colonization but rather active human transport.

Our results provide a good new example of human-mediated colonization of an island by a reptile species in the Mediterranean. This information, together with many other papers, showed how human activities have played a fundamental role in shaping the herpetofauna of several islands and islets in the Mediterranean (Vaccaro et al. 2007; Nogué et al. 2017; Senczuk et al. 2018; Buglione et al. 2019; Faraone et al. 2020; Zuffi et al. 2022; Gallozzi et al. 2023). This is particularly true for volcanic islands, where catastrophic eruptive events occurred in the past causing the extinction of the ancient native populations. Pantelleria island suffered a big volcanic eruption about 45,000 years ago (Agnesi and Federico 1995; Massa 1995; Muscarella and Baragona 2017). Thus, it is likely that most of the reptiles living on the island reached its coasts thanks to passive human-mediated transport as previously observed for *Hemorrhois hippocrepis* (Faraone et al. 2020) and now for *P. siculus*.

To conclude, our study confirms the allochthonous origin of the *P. siculus* population of Pantelleria Island. Thus, even though *P. siculus* is included in the Annex IV of the EU-Habitats Directive and thereby strictly protected by European law, it wouldn't need any population monitoring programme for its conservation on Pantelleria Island.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11756-023-01487-3.

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Author contribution Riccardo Castiglia conceived the study. Data collection were performed by all the authors. Analyses were performed by Carlotta Antinucci and Francesco Gallozzi. The first draft of the manuscript was written by Riccardo Castiglia and all authors commented on previous versions of the manuscript. All authors read, made changes and approved the final manuscript.

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Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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