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Patterns of colour morph diversity across populations of Aegean Wall Lizard, *Podarcis erhardii* (Bedriaga, 1882)

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Podarcis erhardii (Bedriaga, 1882), commonly known as the Aegean Wall Lizard, is a colour-polymorphic island lizard that belongs to the family Lacertidae (Gruber, 1987). Colour polymorphism refers to the presence of two or more genetically-determined colour variants (morphs) within a single breeding population, the rarest of which is too common to be the result of recurrent mutation (Ford, 1945; Gray and McKinnon, 2007). In *P. erhardii*, three monochromatic throat colour morphs (orange, yellow, white; Brock et al., 2020) and their mosaics (orange-white, white-yellow, yellow-orange) occur. Both females and males are colour polymorphic and can exhibit all morph types (Brock et al., 2020). Importantly, this throat colour polymorphism is a trait shared by almost all species in the genus *Podarcis* (Brock et al., 2022), and evidence from genomic studies in *P. muralis* and several other *Podarcis* species has shown that orange, yellow, and white ventral colours are genetically-determined and heritable (Andrade et al., 2019).

Phenotypic polymorphisms are of particular interest to evolutionary biologists because they may play an important role in speciation (Gray and McKinnon, 2007). New species could originate from genetically distinct colour morphs in polymorphic populations, either sympatrically via assortative mating or allopatrically via genetic drift, divergent natural selection on colour morphs, and other between-population processes (West-Eberhard, 1986; Gray and McKinnon, 2007; McLean and Stuart-Fox, 2014). In colour-polymorphic species, the number and frequency of colour morphs among populations generally vary geographically (McLean and Stuart-Fox, 2014), probably due to a combination of divergent local selection and random processes (e.g., genetic drift; Gray and McKinnon, 2007; Runemark et al., 2010). This geographic variation may be an important factor in speciation (Corl et al., 2010; McLean and Stuart-Fox, 2014), as distinct phenotypic morphs may rapidly diverge under different selection pressures in different environments. Different ecologies and environments across a species' distribution may select against certain morphs or favour a particular morph, resulting in reduced morph diversity or morph loss (Takahashi et al., 2011). Here, we document variation in colour morph diversity and frequency across the distribution of the Aegean Wall Lizard.

We recorded colour morph diversity and frequencies on 42 islands and two mainland locations in Greece (Table 1, Fig. 1) over the course of three field seasons (early May to late July in 2017–2019). Our survey methods varied based on island size, which span five orders of magnitude from smallest (Mikri Vigla; area 0.002 km^2) to largest (Naxos; 448 km^2). On small islands that could be walked in a few hours and where lizards essentially represent one continuous population, we sampled across the entire island. At larger islands, we sampled multiple populations from sites that best represented available habitat types on that island, as determined from reconnaissance satellite imagery (Google Earth Engine; Gorlick et al., 2017). Lizards were collected during their diurnal activity periods (08:00–13:00 h and 16:00–18:00 h). We aimed to obtain

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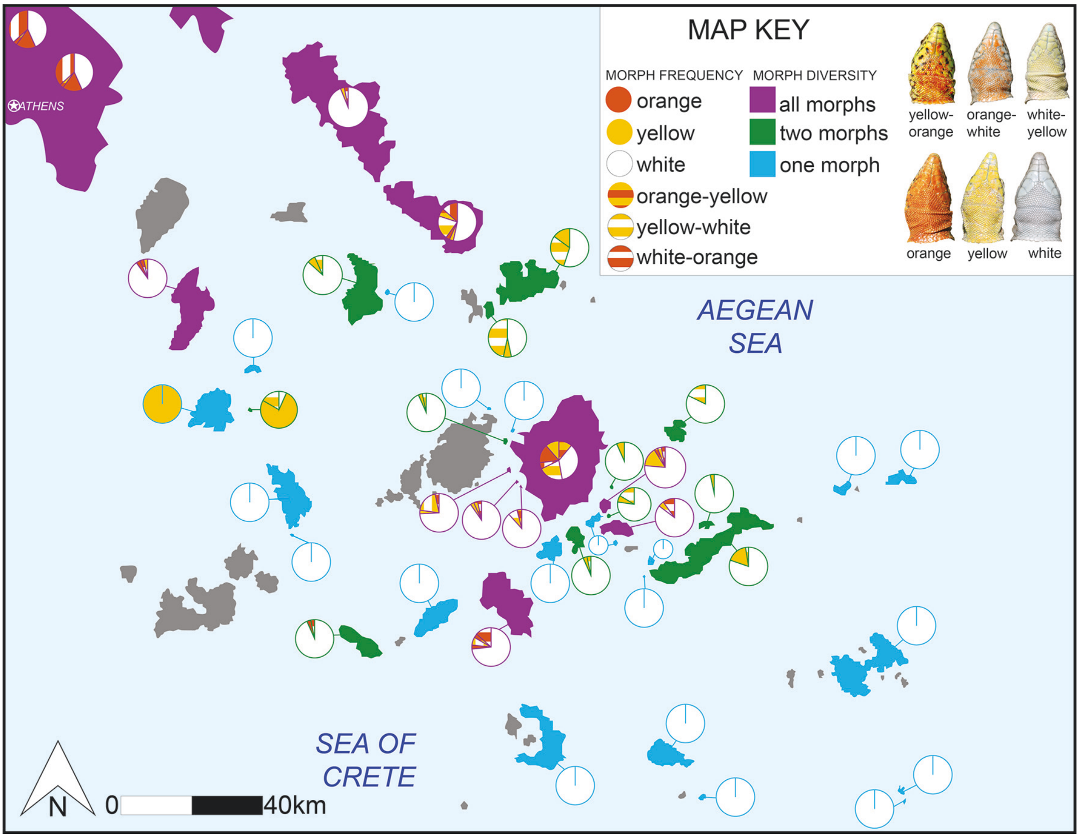

Figure 1. Map of sampling locations (*n* = 44) showing colour morph diversity and their frequencies for the Aegean Wall Lizard, *Podarcis erhardii*. Islands and the mainland are colour-coded by morph allelic diversity, ranging from three (polymorphic = purple) to two (dimorphic = green) to one morph (monomorphic = blue). Morph frequencies are given for each site in pie chart form and colour-coded by morph throat colours (orange, yellow, white, orange-yellow, yellow-white, and white-orange). Islands shown in in grey were not sampled.

a minimum sample size of 30 lizards per population (Corl et al., 2010).

We sampled a total of 1335 lizards at 44 different locations (Fig. 1). We found that colour morph diversity was maintained across islands of varying size and age (Fig. 1). Specifically, 11 of 42 islands and both mainland sites had all three colour morph alleles or some combination of monochromatic and mosaic morphs comprising orange, yellow, and white (13 sites were colour-polymorphic). We observed ten dimorphic populations where only yellow and white alleles, or yellow, white, and white-yellow morphs existed (Table 1), and one island with a dimorphic orange and white population. Of 20 islands with monomorphic populations, 19 were fixed for the white morph and one population, on Serifos Island, was fixed for the yellow morph. Only two islands (Folegandros and Serifos) did not follow the orange-then-yellow pattern of ordered morph loss: Wall lizards on Folegandros are dimorphic and have orange-white or white coloration, whereas on Serifos, they are monomorphic and fixed for the yellow morph.

The ordered morph diversity observed across most of our study islands is similar to that observed by Corl et al. (2010) in the colour polymorphic Side-blotched Lizard, *Uta stansburiana* Baird & Girard, 1852). After sampling 41 populations across the geographic distribution of *U. stansburiana*, these authors found that if a population was missing one morph, it was always the yellow morph, and if a population was missing two morphs, it was always the yellow and blue morphs, and populations with only one morph were always all orange. Even though the ordered-pattern phenomenon in *U. stansburiana* bears similarity to our wall lizard populations, the order in which similar colours are lost or persist differs. What drives geographic variation in morph diversity in these lineages remains an open question. Currently, we do not know if repeated loss of the orange morph in *P. erhardii* represents multiple independent events, as the loss of yellow in *U. stansburiana* (Corl et al., 2010). Given the estimated geomorphological history of island formation by sea-level change (Foufopoulos and Ives, 1999), it is possible that island-level orange morph loss has happened in an independent and repeated fashion. To test this possibility, one could use a population-level comparative approach that considers the evolutionary history of island populations and local variation in ecology and the environment may reveal similar processes driving morph diversity in these species (Corl et al., 2010; Chelini et al., 2021).

We also found an interesting and repeated pattern in colour morph frequencies within populations across the sites we sampled. With the exception of three island sites (Serifos, Vous, and Mykonos), we found that the white morph was always the most common in the population. The white morph was by far the most common monochromatic morph across islands (79% of all lizards, $n = 1335$) followed by the yellow morph (8%), and the orange morph was the least common (3%); this trend was also observed for morph frequencies within populations (Table 1). Furthermore, mosaic morphs (orange-white, white-yellow, and yellow-orange) were usually less common than monochromatic morphs. The most common mosaic morph we found across many sites, by far, was the white-yellow morph (6%), the second most-common was the orange-white morph (3%), and the least common was the yellow-orange morph (1%). Thus, we observed many losses of colour morphs from islands across the archipelago, and the order of morph loss seems to happen in a repeated fashion. In almost every instance when one morph colour allele was lost from an island population, it was always the orange morph (Fig. 1), with the exception of Folegandros. Though morph frequencies and diversity varied across sites, the general pattern that emerged after sampling many distinct, isolated populations was that the white morph is most common and tends to persist longer than other morphs. One possibility is that morph frequencies and overall diversity within and among populations is related to selection, as a completely random process would not likely generate the repeated colour morph patterns observed here. However, in our study we could only report colour morph frequencies in a geographical context. To test for underlying molecular and ecological mechanisms that generate variation in morph diversity, further study of colour morph reproductive behaviour and genetics will need to be done.

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Table 1. Observed colour morph diversity in 44 distinct populations of *Podarcis erhardii*. Populations are listed in alphabetical order with the respective number of individuals (*n*) for each morph, indicated by abbreviations for orange (O), white (W), and yellow (Y) and their combinations (OW, WY, YO). Mainland sites are denoted with an asterisk (*). The most common morph in the population is shown in bold font.

Population	n	O	W	Y	OW	WY	YO
Amorgos	41	0	**33**	7	0	1	0
Anafi	30	0	**30**	0	0	0	0
Andros	33	0	**31**	1	1	0	0
Aspronissi	31	0	**23**	1	1	6	0
Astakida	10	0	**10**	0	0	0	0
Astakidopoulo	10	0	**10**	0	0	0	0
Astypalea	25	0	**25**	0	0	0	0
Delos	15	0	**7**	1	0	7	0
Dhonoussa	17	0	**14**	0	0	3	0
Folegandros	30	0	**28**	0	1	0	0
Gaidouronissi	30	0	**30**	0	0	0	0
Glaronissi	31	0	**24**	0	0	5	0
Gramvoussa	30	0	**30**	0	0	0	0
Ios	30	1	**22**	0	4	2	1
Irakleia	32	0	**32**	0	0	0	0
Kato Koufonissi	26	0	**26**	0	0	0	0
Keros	41	0	**35**	0	4	2	0
Kinaros	30	0	**30**	0	0	0	0
Kisiri	5	0	**5**	0	0	0	0
Kitri Ani	10	0	**10**	0	0	0	0
Kommeno	18	0	**18**	0	0	0	0
Kopria	30	0	**28**	2	0	0	0
Kythnos	30	1	**27**	0	1	1	0
Lazaros	31	0	**31**	0	0	0	0
Levitha	31	0	**31**	0	0	0	0
Mando	30	0	**28**	1	0	1	0
Megalo Fteno	35	0	**35**	0	0	0	0
Mikri Vigla	26	0	**23**	0	0	0	1
Mt. Olympus*	30	4	**13**	1	5	7	0
Mykonos	30	0	11	6	0	**13**	0
Naxos	98	15	**35**	11	5	20	11
Nikouria	30	0	**29**	1	0	0	0
Pano Koufonissi	30	0	**22**	5	1	1	1
Parnitha*	30	8	**8**	0	13	0	1
Parthenos	31	0	**28**	1	1	0	1
Santorini	33	0	**33**	0	0	0	0
Schoinoussa	30	0	**28**	1	1	0	0
Serifopoula	30	0	**30**	0	0	0	0
Serifos	45	0	0	**45**	0	0	0
Sifnos	30	0	**30**	0	0	0	0
Sikinos	30	0	**30**	0	0	0	0
Siros	30	0	**26**	2	0	2	0
Tinos	30	1	**16**	1	4	6	2
Vous	30	0	2	**23**	0	5	0

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