

Phenotypic Polymorphism among Snakes of the Aegean Islands

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Abstract

Within the Aegean Sea, the islands of Alonissos and Skyros in the Northern Sporades, several islands of the Dodecanese, and the islands of Amorgos, Milos, and Sifnos in the Cyclades archipelago have emerged as significant sites of intense adaptive processes involving ophidian taxa such as *Dolichophis caspius*, *Platyceps najadum*, *Elaphe quatuorlineata*, *Zamenis situla*, *Natrix natrix*, and *Macrovipera schweizeri*. These adaptive processes have led to the establishment of distinct polymorphisms, which are examined and discussed in the present study.

Key Words: Phenotypic polymorphism; Colour variation; Island biogeography; Aegean snakes; Adaptive evolution; Melanoticism; Ecological adaptation

Introduction

A substantial proportion of the genetic variation within natural populations remains concealed behind a plastic phenotype, commonly referred to as the wild type, a phenotype particularly well adapted to prevailing environmental conditions. However, my herpetological research on the islands of the Aegean Sea has often allowed me to observe discontinuous phenotypic variations within the same population. The present study documents all recorded polymorphisms and provides considerations regarding their potential adaptive significance.

The author has been engaged in the study of the morpho-biology of Aegean ophidian species since 1981. For each taxon, reference is made to the author's previous publications, which are cited individually in the discussion of the respective species. The scale count values indicated in parentheses represent arithmetic means. For each species, a description of the habitat is also provided, as this parameter is considered essential for the proper interpretation of polymorphism.

Given that, a thorough understanding of the biology of ophidian species is fundamental for their effective protection, several specimens were collected and kept in captivity in order to study their reproductive cycles, developmental timing, and physiological requirements. Detailed investigations of certain aspects of reproductive biology cannot rely on field observations alone, therefore, the information obtained from captive studies is undoubtedly valuable for the development and implementation of conservation strategies aimed at safeguarding these relatively

understudied reptiles [1].

Specimens that died during captivity (whether due to age or other causes) were preserved in alcohol and are now part of the author's personal collection. The described coloration corresponds to that of the living specimens, as alcohol preservation often results in colour fading, particularly in hues derived from carotenoid pigments.

Abbreviations: TL = total length; D = number of dorsal scales at midbody (counted transversely at the midpoint along the total number of ventral scales, the latter being counted according to the classical method); V = number of ventral scales (counted using the classical method, which considers as ventrals those mid-ventral scales that are broader than long); Sc = number of pairs of subcaudal scales (counted starting from the first post-cloacal scale in contact with the contralateral along the caudal midline).

List of studied species

Dolichophis caspius (Gmelin, 1789)

Alonissos Island (Northern Sporades)

(the observations refer to May 1996)

Observed morphs: two - typical and melanistic [5, 2].

Description

Juvenile – 1 specimen (♂).

TL 37,2 cm, D 19, V 199, Sc 109.

Three longitudinal series of black spots are present: one unpaired middorsal series, consisting of transverse bars, and two paired lateral series composed of smaller and less distinct spots, especially in the lower lateral row. All these dorsal spots are arranged alternately along the transverse plane.

Typical morph — 6 specimens (3 ♂♂, 3 ♀♀).

Maximum TL 149 cm (incomplete tail, 23.1 cm) (♂); D 19; V 199–210 (204.5); Sc 99–113 (104.2); $n = 5$.

Background colour greyish-olive; ventral surface pale and immaculate.

Melanistic morph — 1 specimen (♂).

TL 152.6 cm (tail 43 cm); D 19; V 197; Sc 109.

Dorsal surfaces dark, glossy olive-brown, uniform throughout. The dark pigmentation also extends onto the laterally folded portions of the ventral and subcaudal scales, and, though less intensely, spreads over the underside of the head and the distal half of the tail. The remaining ventral surfaces are light yellowish.

Habitat

Probably in response to differing functional requirements, the species was recorded both in relatively warm, dry habitats slightly elevated above the valley floor, and in cooler, more humid valley sites with tall herbaceous vegetation. It was frequently observed thermoregulating on stone walls, particularly those covered with *Smilax aspera*, which it inhabited in the same way as *Malpolon insignitus* on the nearby island of Skopelos.

Remarks

Broggi reported a juvenile melanistic specimen of *Dolichophis caspius* from Alonissos, and Kalogiannis subsequently recorded the presence of this morph both on Alonissos and on the nearby

island of Peristera, which likewise belongs to the Northern Sporades Archipelago [3,4].

It is reasonable to assume that the melanistic morph is already dark at birth, as evidenced by the juvenile specimen reported by Broggi. Kalogiannis also reported, among others, two dark juveniles and two subadults with an even darker coloration suggesting that the dark pigmentation intensifies with age. In contrast, some ophidian species hatch with light coloration and turn black in adulthood (e.g., some Aegean populations of *Natrix natrix*, *Dolichophis jugularis*, and *Hierophis viridiflavus carbonarius*) [3,4].

Further observations on the *Dolichophis caspius* population from Alonissos are provided by Cattaneo [5]. It is worth noting, however, that melanism is an almost unknown phenomenon in this species [6].

Dolichophis caspius (Gmelin, 1789) NISYROS ISLAND (DODECANESE) (the observations refer to May 2006)

Observed morphs: two — typical and spotted [2, 7].

Description

Typical morph – 3 specimens, all ♂♂.

Maximum TL 161 cm (incomplete tail 40 cm), D 19, V 193–199 (196,3), Sc 109 $n = 1$.

A young male, 96 cm long, was already completely devoid of the juvenile dorsal pattern. Remnants of the juvenile habitus usually persist up to a length of about 110 cm, although in females they may remain visible at larger sizes and more noticeably [57,6].



Figure-1 Nisyros Island (Dodecanese): *Dolichophis caspius*, spotted phenotype (photo by M. Grano).

Spotted morph - 1 specimen (♂) (Fig. 1).

TL 157.6 cm (incomplete tail, 37 cm); D 19; V 195; Sc 88 +?.

Two additional exuviae of large ♂♂ specimens, also displayed the characteristic spotted pattern of this morph.

Individuals of this morph retain a black-spotted dorsal pattern even in adulthood.

The spots displayed by these individuals differ from that usually observed in juvenile specimens of the species, as the black pigment covers one or more entire dorsal scales instead being arranged at the edges. The number of spots gradually decreases from the anterior toward the posterior region of the body, fading out around the last third of its length. They represent the outcome of an ontogenetic process distinct from that occurring in typical juvenile specimens.

Habitat

It was found mostly on sunny slopes crossed by paths and featuring stone walls, wire fences, crumbling buildings, and scattered trees and shrubs. In accordance with the species' typical behaviour, individuals were often seen thermoregulating above the stone walls. It also occurred in grazing areas similar in many respects to those described above, though generally drier and less elevated.

Remarks

A polymorphism like the one described above can also be observed in *Dolichophis caspius* from the Ionian island of Corfu [8-11, 56].

An adult specimen of *Dolichophis caspius* displaying a spotted pattern has also been reported from the island of Fourni in the northern Dodecanese [12]. In this individual, dark spots and dark markings are distributed over most of the body, including the head, thereby recalling, at least to some extent, the juvenile habitus. Nevertheless, this chromatic pattern differs markedly from that reported for the spotted phenotypes occurring on Nisyros and Corfu.

It is noteworthy that in the inland area of Kavala (eastern Greek Macedonia), juveniles of *Dolichophis caspius* appear to exhibit two distinct dorsal colour phases: one showing the typical barred pattern, and another displaying a distinct spotting pattern on a lighter background, resembling the coloration of *Hierophis gemonensis* [13].

Further observations on the *Dolichophis caspius* population from Nisyros are provided in Cattaneo [7].

Dolichophis jugularis (Linnaeus, 1758).

Central-eastern Aegean islands and southwestern Turkey

In *Dolichophis jugularis*, colour pattern variation appears related to taxonomic status, sex, and seasonality.

In *Dolichophis jugularis zinneri*, the occurrence of both red- and yellow-bellied phenotypes indicates a polymorphism linked to variation in ventral coloration [14, 16].

Females generally exhibit a less intense coloration, particularly in the subspecies *zinneri*.

During summer, a general fading of pigmentation can be observed, particularly in the Tilos population (subsp. *zinneri*). In some specimens, the fading is so pronounced to reveal a faint spotted pattern, closely resembling that observed in certain specimens of *Dolichophis caspius* from the island of Nisyros [16].

Platyceps najadum (Eichwald, 1831)

Kalymnos Island (Dodecanese)

(the observations refer to May 2004)

Observed morphs: two — typical and melanistic [17] (Fig. 2).

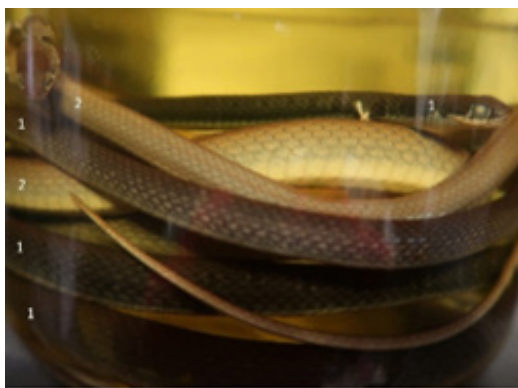


Fig. 2

Figure-2 Kalymnos Island (Dodecaneso): *Platyceps najadum*, melanistic (1) and typical (2) phenotypes.

Description

Typical morphs – 7 specimens.

Size and pholidosis of 2 ♂♂ (respective data):

TL (tail) 66.9 (20.9) cm – 109.5 (30.9) cm; D 19 (18) – 19; V 209 – 205; Sc 126 – 127.

Back grey-olive, belly light. The number of dark spots along the sides of the neck is relatively high. It is noteworthy that specimens of this morph converge in overall coloration with individuals of the immaculate phase of *Eirenis modestus*, both on Kalymnos and on other Aegean islands (for instance, on Samos both exhibit a tawny-ocher hue).

Melanistic morph – 4 specimens.

Size and pholidosis of two ♂♂ (respective data):

TL (tail) 77.7 (23.6) cm – 105.6 (31.3) cm; D 18 – 19; V 207 – 210; Sc 121 – 123.

Background black; ventral surface opalescent grey. Supralabials, infralabials, and mental scales dark wine-red. The number of dark spots along the sides of the neck is relatively high.

Habitat

It was found in sparse steppe covering the island's arid, rocky

slopes. The species appeared to be closely associated with the presence of dry-stone walls.

Remarks

Schneider, based on the examination of two specimens (an adult and a subadult), assigned the *Platyceps najadum* population of Kalymnos to the subspecies *kalymnensis* [18]. This subspecies was originally regarded as differentiated by the pronounced melanism exhibited in adulthood. However, based on my collected data (11 adult specimens belonging to two distinct phenotypes, one typical and the other melanistic) the observed colour variation should instead be attributed not to age, but to a true genetic polymorphism. This, however, does not invalidate the subspecies *kalymnensis*, as it supports the distinctiveness of the local population.

Eirenis modestus (Martin, 1838)

Eastern Aegean Islands and Western Turkey

(observations refer to the month of May)

Recorded morphs: two — immaculatus and *semimaculatus* [12,15,17,28] [19-26].

Description

Immaculate morph – Back uniformly grey, beige, or ocher; belly uniformly cream or yellow. Present in both sexes.

Recorded distribution (number of specimens in brackets): Lesbos (9), Chios (11), Oinousses (10), Samos (13), Fourni (13), Kalymnos (5), Symi (2), inland of Marmaris, western Turkey (3), inland of Bodrum, western Turkey (17), inland of Kuşadası, western Turkey (5).

Spotted morph (semimaculatus) – This morph is characterised by a dark reticulate pattern on the anterior portion of the body. It occurs in both sexes.

Recorded distribution (number of specimens in brackets): Oi-

nousses (6), Samos (1), Leros (1), Kalymnos (2), Symi (3), inland of Marmaris, western Turkey (1).

Habitat

Almost all specimens were collected beneath stones. The species appears to prefer cool, friable soils on hillside slopes, as well as the relatively moist ground of cultivated areas.

Remarks

The Aegean populations of *Eirenis modestus* are assigned to the subspecies *semimaculatus*, described by Boettger on specimens collected on Chios (eastern Aegean) [29]. This taxon is characterised, as previously noted in relation to the spotted morph, by a series of dark spots on the anterior part of the body. Consequently, the epithet *semimaculatus* may also be applied to designate the spotted morph. This spotting observed on the anterior part of the body may be related to the species' habit of partially emerging from its usual refuge (such as a stone wall, rock, or bush). Such blotches might confer a somatolytic effect, or at least enhance camouflage [24].

Specimens improperly described as “melanistic” have been reported from the island of Kastellorizo in the southern Dodecanese [30]. These individuals should instead be regarded as axanthic, in which the absence of superficial yellow pigmentation reveals the underlying melanophores. In the Kastellorizo population, however, the spotted morph appears to be particularly common [30].

Elaphe quatuorlineata (Bonnaterre, 1790)

Amorgos Island (Eastern Cyclades)

(the observations refer to May 1987)

Recorded morphs: two — striped and “concolor” [31, 32] (Fig. 3).



Fig. 3

Figure-3 Amorgos Island (Cyclades): *Elaphe quatuorlineata*, striped (1) and “concolor” (2) phenotypes

Description

Typical morph (four-lined) – 25 specimens: 16 detected in the wild (13 ♂♂, 3 ♀♀) and 9 born in captivity (5 ♂♂, 4 ♀♀).

Specimens observed in the wild: maximum TL 153.3 cm (incomplete tail, 22 cm) (♀); D 23–25 (24.6), V 203–213 (207.8),

Sc 72–74 (73), $n = 2$.

Captive-born specimens: D 21–25 (24.1), V 202–217 (209.8), Sc 40–70 (55.1).

Four dark longitudinal stripes, two medial and two lateral, run

along a beige to ochre dorsal background. On the head, a dark bar extends from the eye to the labial commissure, while the background colour is most pronounced along the vertebral region. The ventral surface is pale yellow.

"Concolor" morph (patternless) – 3 specimens (1 ♂, 2 ♀♀).

Maximum TL 137.1 cm (incomplete tail 12.6 cm) (♀); D 25, V 206–212 (210), Sc 63 $n = 1$.



Figure-4 Amorgos (Island) Cyclades: *Elaphe quatuorlineata*, juveniles of the striped (1) and "concolor" (2) phenotypes

A single specimen, the only offspring produced by a captive pairing of two "concolor" individuals, displayed a distinctly dark coloration on both dorsal and ventral surfaces. It showed broad medial stripes with softly blurred inner margins, which increasingly spread towards the mid-dorsal region anteroposteriorly (Fig. 3). The siblings died before hatching. Assuming that both parents were heterozygous "concolor" for an adaptive mutation in which the concolor allele was dominant, it is plausible that this allele was linked with a recessive lethal factor, such that homozygous concolor individuals would not have survived. Alternatively, a lethal mutation linked to the dominant allele in the germ line of one of the parents might have arisen, in which case only the recessive striped homozygotes would have been able to survive (L. Fanti, pers. comm.).

Habitat

Elaphe quatuorlineata was found mainly along pathways in elevated areas covered by phrygana, interspersed with watercourses bordered by dense stands of *Nerium oleander* and *Vitex agnus-castus*. The species was also observed in the vicinity of cisterns and wells, where it was occasionally seen drinking.

Remarks

The *Elaphe quatuorlineata* population from Amorgos, owing to its distinctive polymorphism, was initially regarded as belonging to a separate species, *Elaphe rechingeri* Werner, 1932. It was subsequently treated as a subspecies of *Zamenis longissimus*, namely *Elaphe longissima rechingeri* Wettstein, 1953. Some years later, Lotze realised that the so-called "concolor" phenotypes were simply patternless individuals of *Elaphe quatuorlineata*, which he classified as *Elaphe quatuorlineata rechingeri*.

All pattern elements are faded, including the temporal bar.

Juveniles belonging to this morph display a markedly reduced dorsal pattern, particularly on the flanks; the reduction becomes more pronounced toward the posterior and the mid-dorsal spots are replaced by narrow transverse bars (fig. 4).

Subsequently, Clark interpreted the occurrence of the two morphs as evidence for the sympatric coexistence of two distinct species, *Elaphe rechingeri* and *Elaphe quatuorlineata* [33,34].

Captive breeding specimens from Amorgos has demonstrated that several colour and pattern phases may arise within a single clutch, yielding striped, uniform, and partially patterned offspring [35].

In the patternless "concolor" phenotypes, a genetic mutation may inhibit or prevent the production of the enzyme that catalyses the synthesis of the black pigment. These genotypes appear to be dominant, and according to simple Mendelian inheritance, the production of striped offspring (in a 1: 4 ratio) would occur only through the mating of two heterozygous individuals carrying the recessive "striped" allele (see above, "Description of the concolor morph"). In this regard, Mayr (1963) writes: "... morphic genes are selected in many cases for their physiological effect; a gene that is recessive for its morphological contribution to the phenotype may be dominant with regard to its physiological phenotype; this dominance may allow the rapid spread of a morphologically recessive gene".

On the other hand, given the particular environmental conditions of the Aegean islands (characterised by a relatively warm and dry climate) these monochromatic individuals might represent well-adapted ecophenotypes, in which the "concolor" and "striped" traits may be expressed phenotypically only below or above certain humidity thresholds (a threshold phenomenon). In this regard, Suzuki et al. wrote: "An organism may fail to express the phenotype normally associated with its genotype due

to the presence, within the genome, of a modifier, an epistatic gene, or a suppressor, or as a result of the modifying influence of the environment [36].

“Concolor” phenotypes of *Elaphe quatuorlineata*, in addition to those found on Amorgos, have also been recorded by me on the Cycladic islands of Kea and Naxos [37,32]. They also appear to occur on the mainland, for example in Bosnia [38].

Zamenis situla (Linnaeus, 1758)

Milos Island (SW Cyclades)

(the observations refer to May 1983)

Observed morphs: two — *leopardinus* and *situla* [2, 39].

Description

Spotted morph (leopardinus) – Four specimens (1 ♂, 3 ♀♀), all captive-born.

Maximum TL 103.3 cm (♀); D 23–27 (24.5); V 231–246 (240.5); Sc 61–66 (63.3).

Dorsal ground colour olive-grey. In addition to a median dorsal series of large brick-red spots bordered with brown, the flanks bear additional series of smaller, more diffuse spots. Furthermore, the back is traversed by four longitudinal dark stripes two medial (more developed) and two lateral, slightly overlapping the dorsal spots. The belly is yellow, marked with black spots.

Striped morph (situla) – 19 specimens: 8 observed in the wild (6 ♂♂, 2 ♀♀) and 11 born in captivity (2 ♂♂, 9 ♀♀).

Specimens observed in the wild: maximum TL 118 cm (♀); D 25–28 (26.8); V 230–248 (236.7); Sc 71–87 (81.3).

Captive-born specimens: D 21–27 (25.1); V 235–248 (242.4); Sc 49–86 (66.1).

Usually larger in size than the spotted morph. The dorsal surface of the body bears two longitudinal brick-red stripes bordered in black; in females the stripes are interconnected by transverse bars of the same colour forming a ladder-like pattern. The dark longitudinal bands are absent. In all other respects, this morph resembles the previous one.

Habitat

It seems to inhabit open habitats with sparse vegetation [40].

In earlier times, Milos probably had more abundant water resources and a comparatively more extensive plant cover than it has today. In his checklist of the flora of the nearby island of Sifnos, Malakates mentions several species typical of moist habitats, such as riverbanks and grassy meadows, some of which are no longer present on Sifnos today [27, 41]. Therefore, Sifnos was once much richer in vegetation and water sources, as clearly evidenced by the flora recorded by Malakates [41]. It is therefore plausible to assume that, in the past, Milos experienced a more humid climate. Evidence of this can be found in historical records showing that, during the Roman period, the island exported products such as honey, wine, and olive oil.

Remarks

All the pattern variations displayed in *Zamenis situla* throughout its range can ultimately be grouped into two principal types: the spotted (*leopardinus*) phenotype and the striped (*situla*) phenotype. In fleeing individuals of the spotted morph, the dark longitudinal bands overlaid on the spots can produce a phenochromatic effect, making these snakes easily mistaken for those of the *situla* morph. These overlying stripes may therefore have an selective-adaptive function. In specimens of the *leopardinus* morph, these same dark stripes remain visible even on the exuviae, closely resembling the exuviae of *Elaphe quatuorlineata*. The *leopardinus* morph appears to be the most widespread across all the Aegean islands, with the exception of the Cycladic island of Milos, where it now seems to be relatively rare. Schweizer [40, 42], referring to the herpetofauna of Milos, however, appears to indicate that the spotted morph was more common than the striped one. Obst et al. and Schulz, however, report that on Milos the striped form predominates, if not exclusively. In my own fieldwork, I have found only *situla* specimens [43,35].

The ratio between the two phenotypes (*leopardinus* / *situla*) observed in offspring born in captivity from a pair of *situla* specimens originating from the island of Milos consistently favoured the striped form in every generation, with an overall proportion of 1: 4 over six consecutive breeding years (Table 1). In addition to Milos, I have personally observed the *situla* morph on the islands of Thassos and Samos (on the latter, the striped form is also represented in the local natural history museum). Intermediate pigmentation forms appear to occur on Skyros [5, 26, 44] (Fig.5).

Table 1. Captive breeding record of a pair of *Zamenis situla* (*situla* phenotypes) from Milos Island (SW Cyclades).

year	laid eggs	unhatched eggs	hatchlings
1987	3	-	1 <i>leopardinus</i> 2 <i>situla</i>
1988	4	1	3 <i>situla</i>
1989	7	1	2 <i>leopardinus</i> 4 <i>situla</i>
1990	6	3	1 <i>leopardinus</i> 2 <i>situla</i>
1991	6	-	6 <i>situla</i>
1992	8	7	1 <i>situla</i>



Fig. 5

Figure-5 Skyros (Island) (Northern Sporades): *Zamenis situla*, phenotype intermediate between the *situla* and *leopardinus* morphs.

Based on my own field and captive observations, it appears that the two phenotypes of *Zamenis situla* also differ in their responses to various environmental conditions. The striped phenotype appears to be the less specialized of the two. It is usually the first to hatch in mixed clutches, tends to be less elusive and shows greater boldness and initiative when hunting (regularly consuming not only nestling mice but also weaned ones), and most notably it demonstrates a higher tolerance to hot, arid environmental conditions. This latter feature also appears to occur in other “striped” snake species when compared with their respective homologous species. For instance, *Elaphe quatuorlineata* shows a greater affinity for warm and arid environments than *Elaphe sauromates*, and *Zamenis lineatus* likewise exhibits a stronger xerothermophilous tendency than *Zamenis longissimus* (pers. obs.). The striped phenotype of *Chalcides chalcides* (as compared to the “concolor” form) also seems to support this trend, reflecting adaptation to climatic conditions that are progressively shifting toward higher xerothermic environments. Based on these observations, the two phenotypes of *Zamenis situla* may alternate in time and space in response to changing environmental conditions (transeunte polymorphism, *sensu* Ford, 1940) [45]. In this case, spots and stripes could represent neutral expressions of linked genes that together produce a specific adaptive response (such as a physiological one) to a particular environmental factor. Supporting this present hypothesis, Schweizer’s observations indicate that, during the 1930s, the striped morph on Milos was much less common than it is today, while the spotted morph predominated, presumably in association with more humid environmental conditions [40, 42].

***Natrix natrix* (Linnaeus, 1758)**

Skyros Island (Northern Sporades)

(the observations refer to May 1993)

Observed morphs: five — melanistic, *moreoticus*, *persa*, spotted and “subconcolor” [5, 2].

Taxonomic note

Until recently, most of Greek populations of *Natrix natrix* were assigned to the subspecies *Natrix natrix persa* (Pallas, 1814), a taxon essentially characterised by two light stripes running along the back. Based on combined mitochondrial and nuclear genomic evidence, the populations from the southern Balkans, western Anatolia, and Cyprus are now recognized as *Natrix natrix moreotica* (Bedriaga, 1882), with the type locality in northern Peloponnese [47]. Consequently, *Natrix natrix persa* (Pallas, 1814) is now regarded as a junior synonym of *Natrix natrix scutata* (Pallas, 1771), a taxon with a more easterly distribution.

Description

Melanistic phenotype – 3 ♂♂ (Fig. 6).

Maximum TL 56.5 cm; D 19; V 178–182 (179.6); Sc 70–72 (71) ($n = 2$).

Melanisation of the dorsal ground colour is variably advanced but always sufficient to conceal the usual pattern; the light collar spots visible. The lower parts shows a black pattern that becomes progressively more extensive from front to rear, eventually covering the entire tail.

moreoticus phenotype – Similar to the melanistic phenotype but with two light stripes running along the dorsum [48].

persa phenotype – 2 ♂♂ (Fig. 6).



Figure-6 Skyros Island (Northern Sporades): *Natrix natrix*, melanistic (1), “*persa*” (2), and “*subconcolor*” (3) phenotypes. The coloration of the “*subconcolor*” phenotype was markedly altered by alcohol preservation compared to that seen in the wild.

Maximum TL 62.5 cm; D 19; V 177–178 (177.5); Sc 69–75 (72). Dorsal surface grey-olive, marked with 4–6 longitudinal rows of small, irregular, and fringed black spots. The light spots of the collar are variably distinct, while the dark spots behind them are always well defined. Two relatively faint, not very pronounced pale stripes extend longitudinally along the back; the ventral surface shows the typical pigmentation pattern of the species.

Spotted phenotype – 1 juvenile.

Similar to the *persa* phenotype, but lacking the two pale longitudinal dorsal stripes (see also Buchholz & Schultze Westrum, 1964).

“subconcolor” phenotype – 1 ♀ (Fig. 6).

TL 62.5 cm; D 19; V 173; Sc 50.

Similar to the spotted phenotype, but with a slightly darker dorsal ground colour, just enough to overlay the small, faint spots of the pattern. In addition, many of the dorsal scales have partially pale-edged margins.

Habitat

It was found in areas consistently well exposed to sunlight, yet generally with a fair degree of moisture: among grasses, at the base of stone walls not far from active streams or cisterns, along riverbanks, and beneath well covers near settlements. It was only rarely encountered in dry habitats.

Remarks

The melanistic phenotype has also been observed by me on the islands of Kea, Milos, Mykonos, Antiparos, and Samothraki. On Kea, grass snakes that develop melanism in adulthood tend to display four rows of relatively small, rounded dorsal spots (*fusca* morphotype) [37]. On Milos, a large portion of the *Natrix natrix* population consists of individuals that turn black within the first 12–18 months of life, (*schweizeri* morphotype) [49].

I have also observed the *persa* phenotype on the islands of Antiparos, Paros, Naxos, Thassos, Samothraki, Chios, Samos, and Rhodes. With the exception of Thassos and Samothraki (in the northern Aegean), where individuals exhibit six longitudinal rows of dark, irregular, and fringed dorsal spots, specimens from the other islands display only three rows of dark dorsal spots, though with the same general characteristics.

I have also recorded the spotted phenotype on the islands of Milos (morphotype *schweizeri*) and Mykonos. Individuals of this phenotype exhibit three rows of dorsal spots, which are more

rounded than those observed in the *persa* phenotype.

In summary, the *Natrix natrix* population on the island of Skyros is composed of individuals that do not attain large sizes, display a low number of subcaudal scales in both sexes, and bear 4–6 longitudinal rows of dark dorsal spots. A high proportion of melanistic individuals is present (over 45% of the observed specimens), and, as noted, the population displays pronounced polymorphism. This is likely a population undergoing incipient evolution, similar to what occurs on Skyros with *Elaphe quatuorlineata* and on the nearby island of Alonissos with *Dolichophis caspius* and *Vipera ammodytes* [5, 2, 54]. Within the Northern Sporades, Skyros and Alonissos, the two islands farthest from the Greek mainland, appear to be those where the most intense microevolutionary processes have occurred, likely due to the absence or extreme reduction of gene flow.

Thus, on Skyros there are at least five distinct phenotypes: two dark forms (melanistic and *moreoticus*) and three light ones (*persa*, spotted and “subconcolor”). It is worth noting that while the melanistic specimens were observed to be active mainly during the early morning hours, the grey-olive individuals were most frequently encountered in activity during the central hours of the day. The darker individuals may, in fact, begin their activity earlier than the others, as they are able to thermoregulate more quickly.

This would allow the exploitation of resources at different times, thereby reducing intraspecific competition. In summary, the polychromy of *Natrix natrix* on Skyros could represent a compelling example of adaptive ecological polymorphism. These considerations may also apply to all populations that display polymorphism characterized by black or dark-coloured individuals.

Macrovipera schweizeri (Werner, 1935).

Sifnos Island (Cycladen)

(the observations refer to the months of April–May 1981 and May 1985)

Observed morphs: two — greyish and ocher [39, 46].

Description

All colour variations (seasonal, sexual, individual, or age-related) can be traced back to two fundamental phenotypes, distinguishable almost from birth: the greyish and the ocher morphs. *Greyish morph* – 10 specimens (7 ♂♂, 2 ♀♀, 1 juv.) (Fig. 7).



Figure-7 Sifnos Island (Cyclades): *Macrovipera schweizeri*, greyish morph (photo by F. Paysant).

Maximum TL 145.3 cm (♂); D 22–25 (23.1), V 154–159 (156.2), Sc 31–44 (39.6) ($n = 6$). *Ocher morph* – 10 specimens (7 ♂♂, 3 ♀♀) (Fig. 8).



Fig. 8

Figure-8 Sifnos Island (Cyclades): *Macrovipera schweizeri*, ocher monochrome morph (photo by F. Paysant).

Maximum TL 135.7 cm (♂); D 24–25 (23.3), V 154–163 (157.2), Sc 37–43 (40.7) ($n = 7$).

In spring, adult ♂♂ (especially the larger ones) reach the peak of a darkening process that begins in autumn (as observed in captivity), probably in response to the seasonal temperature drop, as lower temperatures tend to induce darkening in reptiles. The background of these reproductive ♂♂ exhibit a dorsal coloration shifting toward dark brown and reddish tones, such that the two phenotypes are not always easily distinguishable. The darkening ends with the shedding that occurs in July, when the two phases once again become clearly distinguishable (as observed in captivity).

The dorsal pattern of the Sifnos viper generally appears faded and blurred; the dark bands along the back and sides often tend to turn into diffuse spots with poorly defined margins. The fading of the pattern reaches its peak expression in the ocher phenotype (specimens of to this morph completely devoid of any dorsal ornamentation have been observed Fig. 8).

In the greyish phenotype, the ventral coloration is often enriched with tawny hues, while in the ocher phenotype, isabelline tones prevail.

Habitat

It inhabited dry-stone walls with poor vegetation at their base, especially those facing old abandoned houses and/or interrupted by small stone shelters, often bordered, or sometimes not, by large shrubs of *Pistacia lentiscus*, which were probably used as visual landmarks aiding individuals in locating mates. The dry-stone walls were mostly aligned parallel to the prevailing winds (thus providing sheltered interiors) and typically bordered fallow fields not far from cultivated areas, which were rich in small mammals.

Remarks

The two phenotypes, greyish and ocher, appear to be in selec-

tive equilibrium, as the ratio observed during both survey periods (1981 and 1985) was 1:1. In fact, the two morphs proved to be cryptically adapted to different type of substrates within the same habitat. Moreover, considering that on Sifnos spring is much shorter than summer, yet equally dangerous for vipers due to their increased exposure, the greyish morph may be more advantaged during spring, as its coloration blends more effectively with the prevailing seasonal hues. Conversely, the ocher morph would gain the upper hand in summer for the same reasons. Among the juveniles born in captivity, the ratio between the two phenotypes was likewise equal.

***Macrovipera schweizeri* (Werner, 1935).**

Milos Island (SW Cycladen)

(the observations refer to May 1983)

Observed morphs: two — greyish and erythrochroic [39, 46].

Description

Greyish morph — 47 specimens (21 ♂♂, 8 ♀♀, 18 juv.).

Maximum TL 127.8 cm (incomplete tail: 12.9 cm) (♂); D 19–25 (22.7), V 140–158 (150.9), Sc 31–45 (39.9) ($n = 36$).

The overall coloration is greyish-brown. The pattern is weakly defined, consisting of large, dark spots or subrectangular bars, transversely arranged along the back and vertically along the flanks, alternating and often separated by a pale longitudinal line. The belly is densely speckled on an isabelline background, frequently suffused with reddish hues. The tail becomes progressively more yellowish toward the tip. After shedding, lighter ash-grey tones emerge making the pattern more distinct.

Erythrochroic morph – 1 specimen (♂).

TL 62.7 cm (incomplete tail 6.5 cm); D: 23; V: 156; Sc: 32 + ?
Back coloration: uniform brick-red coloration.

Habitat

Macrovipera schweizeri is a frequent user of dry-stone walls, anthropogenic structures that offer it protection, shelter, and iso-

lation from external factors. Dense mastic shrubs (*Pistacia lentiscus*) bordering the dry-stone walls, fallow fields grass in their surroundings, and the shrubby or herbaceous vegetation occurring at their base, represent additional components of the habitat preferred by these vipers. Occasionally, near the dry-stone walls, there are dilapidated abandoned houses that *Macrovipera schweizeri* might visit for feeding purposes (as they are highly frequented by rodents) or use as visual landmarks for mating encounters. In addition, a typical habitat observed on Milos consists of stone piles bordering dirt roads where vipers have been observed.

Remarks

According to Schweizer, erythrocric individuals of the Milos viper can be found in elevated areas featuring watercourses and reddish rock formations, which are thus homochromic with the snake's pigmentation [40, 49]. In certain localities, they do not appear to be rare, while in others (where the other morph is very common) they seem to be completely absent. The only erythrocric specimen I recorded was observed in the locality of "Parasporos", perfectly coiled on a light-coloured stone. In that area, where the greyish morph was, at the time, particularly common, I did not observe any reddish soils. This suggests that these erythrocric phenotypes, though uncommon, are scattered throughout the island.

This morph appears to be prevalent, if not exclusive, in the male sex [40, 42]. In snakes, the male is the homogametic sex; therefore, it is reasonable to assume that these individuals, characterized by such a beautiful yet rare coloration, are homozygous recessive for the genes involved in the expression of this pigmentation [50].

It must be taken into account that, whereas mutation-derived alleles, when recessive, tend to occur at low expression frequencies or remain unexpressed in open populations, in insular populations reproductive isolation and repeated inbreeding among the descendants and relatives of the original colonizers, combined with the lack of gene flow from the parental population, may increase the expression frequency of such alleles. This may occur as a result of intrinsic biochemical processes and/or epistatic interactions with other components of the genotype controlling their phenotypic manifestation. Consequently, characteristics that were previously rare may, through random processes such as genetic drift, become common within isolated populations, and vice versa.

Concluding Remarks

According to Ford, genetic polymorphism is defined as the condition in which two or more distinct forms of the same species coexist within a single population, in proportions such that the rarer form cannot be maintained merely through recurrent mutation [51].

Polymorphism is generally considered to be adaptive, as it enables a population to better withstand environmental fluctuations than would be possible with a single genotype or a single co-

adapted gene complex. In certain instances, however, morphs appear to be selectively neutral. In such cases, neutral traits may be closely linked to others that are of high adaptive value (for example, at the physiological level) thereby increasing the fitness of their carriers.

Concerning the polymorphism displayed by *Natrix natrix* on the island of Skyros, we have discussed the importance, within a population, of the presence of melanistic phenotypes. Their presence may allow the different morphs to exploit environmental resources at different times throughout the day (melanistic phenotypes, due to their darker coloration, are able to thermoregulate more rapidly than the others thus enabling earlier onset of activity).

Some morphs appear to be maintained by some form of balancing selection, involving opposing selective forces. For example:

- one morph is favoured during one season but experiences unfavourable selection in another (as in the case of the *Macrovipera schweizeri* population on the island of Sifnos);
- different morphs are able to exploit different environmental conditions within the same habitat, thereby reducing competition and selective elimination (as in the case of the *Macrovipera schweizeri* population on the island of Milos);
- one morph is favoured under environmental conditions characterized by a certain degree of humidity, and experiences negative selection as these conditions become drier. It is the case of the presumed transeunte polymorphism of the *Zamenis situla* population on the island of Milos, possibly induced by changes in the physical environment due to anthropogenic, climatic, or hydrogeological factors, which could have led to a sudden shift in the selective values of the two competing phenotypes (see *Zamenis situla*, "Habitat" and "Considerations").

In conclusion, polymorphisms, being the most striking examples of variation within a population provide valuable insight into the mechanisms underlying species adaptation to their environment.

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