BIOGEOGRAPHIA
The Journal of Integrative Biogeography

Biogeographia – The Journal of Integrative Biogeography 2025, 40 (2): a051

https://doi.org/10.21426/B6.50587

Distribution and habitat suitability of *Zamenis longissimus* exhibiting dark colourations, with a new record from Northwestern Italy

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Keywords: colour anomaly, Colubridae, Europe, habitat suitability, melanism, snake.

SUMMARY

Dark colour aberrations in reptiles are rarely mapped and poorly understood. We document the first axanthic-like Aesculapian snake (*Zamenis longissimus*) from Lombardy, Italy, and merge this record with 44 earlier reports from the literature and iNaturalist. An ensemble ecological niche model calibrated with three uncorrelated WorldClim variables (i.e., mean annual temperature, mean diurnal temperature range and annual precipitation) achieved good performance (AUC = 0.84 ± 0.04; TSS = 0.58 ± 0.08). Mean diurnal temperature range emerged as the strongest predictor, with suitability increasing in warmer regions that experience smaller day–night thermal amplitudes. Predicted hotspots for the dark morph include the Atlantic coasts of Spain and France, the Tyrrhenian margin from Liguria into Piedmont, the eastern Adriatic littoral, and Black Sea coastlines of Russia, Georgia and Turkish Thrace. These areas largely coincide with published and citizen-science records, lending confidence to model outputs despite the sparse dataset. Anyway, the genetic basis and fitness effects of this colour remain untested; directed surveys and molecular work in the predicted zones are now needed. Our map offers a concise guide for future sampling.

INTRODUCTION

Colouration is a key aspect of an organism's ecology, playing crucial roles in thermoregulation, social communication, ultraviolet protection, antipredatory defense and parasitic exploitation (Bechtel 1995, Vitt and Caldwell 2014, Cuthill et al. 2017; Storniolo et al. 2021). Colours are produced by pigments, nanostructures or both (Shawkey and D'Alba 2017). In reptiles, the pigment cells in the skin develop embryologically from the neural crest and are called chromatophores (Bechtel 1978, Lotti 2011, Vitt and Caldwell 2014). Chromatophores can be distinguished according to the colour they reflect under white light. Melanophores are the most common type and are scattered across the basal layer of the epidermis; they contain melanosomes filled with melanin and are responsible for dark colourations. Xanthophores are found in a single layer under the basal lamina of the epidermis and are responsible of yellow, orange and red colouration, due to their content of pteridines and carotenoids. Finally, beneath the xanthophores, 2-4 layers of iridophores are present; these cells reflect light, giving animals an iridescent appearance (Bagnara et al. 1968, Bechtel 1995, Lotti 2011, Vitt and Caldwell 2014).

Colour aberrations, which are caused by chromatophore disorders (Bechtel 1995), are usually non-adaptive and thus eliminated by natural selection (Andrén and Nilson 1981). However, there are conditions in which these mutations become adaptive and increase individuals' fitness (Clusella Trullas et al. 2007, 2008, Moreno Azócar et al. 2020). Axanthism is an understudied colour aberration, reported as a hereditary defect of xanthophores that lack or show a marked reduction in pteridines, resulting in blue, blueish, grey and dark to very dark patterns and eyes (Bechtel 1995, Lotti 2011, Jablonski et al. 2014). To date, so-called axanthism is reported only in a few reptile species in nature (Bechtel 1991, Cattaneo 2015, Cavalcante and Bruni 2018, Borteiro et al. 2021, Allain et al. 2023).

The Aesculapian snake, *Zamenis longissimus* (Laurenti 1768), is a monotypic colubrid species found in mainland Europe, from Northeastern Spain to Asia Minor (Venchi and Luiselli 2011, Geniez 2018, Di Nicola et al. 2021). In Italy, it occurs throughout most of the continental and peninsular regions, with its Southern distribution limit in Latium and Molise, and it is also present on Elba Island (Venchi and Luiselli 2011, Di Nicola and Vaccaro 2020, Di Nicola et al. 2021). In Apulia, some populations exhibit an intermediate phenotype between *Z. longissimus* and *Zamenis lineatus* (Camerano 1891), the latter endemic to southern Italy and Sicily (Salvi et al. 2017). The Aesculapian snake undergoes an ontogenetic change of phenotype, with juveniles having a grey-brownish dorsal background colour with dark irregular patches, a well-defined light-coloured collar, and a dark spot between the postocular scales and the temporal region. Adults display a more uniform pattern, with colourations ranging from yellow-brownish to olive and tawny grey, small white spots on the scale borders, and a faint stain in the temporal region. The ventral region ranges from white to yellowish and brownish (Venchi and Luiselli 2011, Geniez 2018, Di Nicola et al. 2021).

Although *Z. longissimus* is a widespread species, only few cases of so-called axanthism or other similar colour aberrations are reported in the wild in the scientific literature (Table 1). Although this colour anomaly is already reported across Europe (Fig. 1), this work provides the first report of an axanthic-like individual from Northwestern Italy.

Understanding the distribution of such rare colour morphs in wild populations poses significant challenges, especially given the scarcity of documented cases. For this reason, ecological niche models (ENMs) represent an effective tool for exploring the potential distribution of rare phenotypes. These models relate occurrences of a given species, or in this case individuals with specific phenotypic traits, to environmental data in order to predict their distribution. Recently, these models have been proved to be a valuable tool for predicting the distribution of rare or endangered reptile and amphibian taxa (e.g., Ficetola et al. 2020, Di Nicola et al. 2023, 2024), and have also led to the discovery of new populations of threatened species (Mizsei et al. 2016).

In this work, we gathered all known cases of dark colour aberrations in wild Aesculapian snakes, as reported both in the scientific literature and on the citizen science platform iNaturalist. We then use these data to compute an ensemble ecological niche model, with the aim of predicting the potential distribution of wild aberrant *Zamenis longissimus*.

MATERIALS AND METHODS

Field sampling

On 28th March 2025 at 14:30, a colour-aberrant adult female *Z. longissimus* was spotted basking in grass near a watercourse in proximity of Pavia, Lombardy, Italy (approx. coordinates 45°10' N, 9°10' E; elevation 60 m above sea level). The weather was clear, and the temperature was about 18.5 °C. Species identification was made on morphological basis and the sex was determined according to tail length and the shape of the cloacal region (Venchi and Luiselli 2011, Di Nicola 2019, Di Nicola et al. 2021). To minimize handling stress, all measurements were obtained from detailed macro photographs analysed using ImageJ 1.54k (Schneider et al. 2012). The following measurements were recorded: tail length (TL, from the cloaca to the tip of the tail) and total length (TotL, from the tip of the rostral scale to the tip of the tail). The snout-vent length (SVL, from the tip of the rostral scale to the cloaca) was derived as the difference between TotL and TL.

Occurrences and study area

The database used for the ENM was created by merging the observations reported in the scientific literature [i.e., only Zadravec and Lauš (2011) reported the coordinates] and the occurrences from iNaturalist (inaturalist.org, accessed on 7th April 2025).

All *Z. longissimus* occurrences were manually inspected, and only eligible observations were included in the dataset. Eligibility criteria for aberrant snakes were as follows: i) dark colouration (i.e., grey, greyish or black/blackish dorsal scales); ii) absence or marked reduction of yellow/yellowish pigment, resulting in a white gular region and anterior ventral scales; iii) dark to blackish ventral scales; iv) dark to blackish eyes; and v) a dark to black spot in the temporal region (see Fig. 2 for references). Observations for which the photographs did not allow certain classification were excluded. In addition, a single observation from the Canary Islands (not part of the native species range or known introduced populations, e.g., United Kingdom) was not included in the database. All records with a coordinate accuracy greater than 4 km were excluded and finally, only one observation for raster cell was retained for modeling. The resulting dataset comprised 45 records of dark coloured Aesculapian snakes.

To obtain the vector layer used as the study area, all iNaturalist research-grade occurrences with coordinates accuracy less than 20 km were downloaded from the Global Biodiversity Information Facility (GBIF.org 2025). All downloaded occurrences were imported into QGIS 3.34 (QGIS.org 2025) and the study area was generated using the minimum convex hull of the observations. This layer was then manually refined to better fit the actual distribution of the species.

Ecological niche modelling

The potential distribution of dark coloured *Z. longissimus* was estimated in R 4.4.1 (R Core Team 2024) using the *biomod2* package (Guéguen et al. 2025).

Predictor variables used for modelling were downloaded at a 30 arc-second spatial resolution from the WorldClim 2.1 database (Fick and Hijmans 2017) and consisted of 19 bioclimatic layers (bio1 - 19). The bioclimatic variable selected as predictors were mean annual temperature (bio1), mean diurnal temperature range (bio2) and annual precipitation (bio12). Pairwise Pearson's correlation tests were performed to check for collinearity among the selected variables. No pairwise comparisons showed any significant correlation ($|r| < 0.25$). Bioclimatic variables were then cropped on the study area layer.

To generate a more accurate projection, an ensemble model was developed by integrating several single ENMs (Araújo and New 2007). The final model consisted in an ensemble of five different algorithms: Artificial Neural Network (ANN; Friedman et al. 2000), Generalised Additive Model (GAM; Hastie and Tibshirani 1987), Generalised Boosting Model (GBM; Ridgeway 1999), Generalised Linear Model (GLM; Nelder and Wedderburn 1972) and Maximum Entropy (MAXENT; Phillips et al. 2004). All algorithms were tuned with the "bigboss" pre-defined parameter. For each algorithm, a set of 10,000 pseudo-absences was randomly generated. Models were developed with a random cross-validation procedure repeated ten times; in each cycle, the whole dataset (i.e., occurrences plus pseudo-absences) was split, with 75% used for calibration and 25% for validation. Variable importance was estimated through five permutations. All models were evaluated based on the area under the curve (AUC) and the true skill statistic (TSS). The former is a threshold-independent measure of discrimination between presence and background points (Fielding and Bell 1997), while the latter measures the prediction success rate of a model using occurrences and pseudo-absences (Allouche et al. 2006). AUC values range from 0.5 to 1, with values greater than 0.75 indicating good model quality and values above 0.9 indicating excellent models (Fielding and Bell 1997). TSS values range from -1 to 1, with values above 0.4 considered fair, above 0.6 good and above 0.8 indicating excellent models (Ben Rais Lasram et al. 2010). The ensemble model was built using the weighted mean algorithm (i.e., the better a single model performed, the more weight it was given in the ensemble), retaining single models with AUC > 0.75. To set the minimum suitability values for model projections, the AUC threshold was used. Models were tested for overfitting by assessing the difference between the calibration AUC value (AUC_{cal}) and the validation AUC value (AUC_{val}) (Warren and Seifert 2011).

RESULTS

Colour aberration description and distribution

The Aesculapian snake observed in Lombardy exhibited a dark grey dorsal colouration with white spots on the edges of the dorsal scales (Fig. 2A-C), and a dark grey head with the spot in the temporal region being completely black (Fig. 2B). The ventral region was white under the head, fading to black at approximately mid body (Fig. 2B-C). Only a few normal yellowish spots were visible on the head and ventral region (Fig. 2B-D). The snake measured 109 cm (SVL = 88 cm, TL = 21 cm).

According to the scientific literature, aberration tending toward axanthism have been recorded in Bosnia-Herzegovina, Bulgaria, Croatia, France, Greece, Hungary, Italy, Montenegro, Romania, Russia, Slovenia and Spain, with some observation dating as early as 1897 (see Table 1 for further details). Observations from the iNaturalist database also report the presence of this colour anomaly in Austria, Serbia and Turkey (Fig. 1).

Table 1. Colour aberrations tending to axanthism reported in the scientific literature; * refer to references for which we were not able to access the full text but were included and analysed within one or more references of the consulted literature.

Reference	Observation type	Location	Description
Fitzinger 1826	General description		
Dürigen 1897	Descriptive	Dalmatia (Trieste), Naples, Slovenia, Croatia, Bosnia-Herzegovina	
Werner 1897*			
Marchi 1901	Descriptive	Italy (Alps)	Totally black
Boulanger 1913	General description		Black on dorsal and ventral scales or blackish-grey to black above and dark grey beneath, with the angular line of each side of the ventral scales remaining light
Steinheil 1913	Illustration	Bosnia-Herzegovina (Banja Luka)	Intense black dorsal scales with withe spots, white gular region fading to a grey ventral
Angel 1946	General description	France	Black or grey-blackish dorsal with a light line on each side of the gular region
Vogel 1968*		Bulgaria	
Cattaneo 1975	Images	Italy (Castelfusano)	Brownish-black dorsal with white spots, brownish-black head, with dark line in the temporal region, black or black-greyish ventral
Street 1979	General description	Hungary (Zemplén)	Black both on dorsal and ventral scales or grey
Bruno 1984	General description	Italy	
Meinig and Schlüpman 1987	Images	Spain (Cantabrian mountains)	Totally black
Bruno and Maugeri 1990	Illustration		Black dorsal with white gular region
Schulz 1996*		Russia (Sochi)	
Bologna 2000*			
Cattaneo 2005	Images	Italy (Castelporziano)	Black or blackish both dorsally and ventrally with a white gular region
Kreiner 2007	Images	Southern Romania	Dark grey colouration with black line in the temporal region, with a few normal yellow spots, white gular region
Stojanov et al. 2011*		Bulgaria	
Zadravec and Lauš 2011	Images	Croatia (Krk)	Dark grey colouration with black line in the temporal region, with a few normal yellow spots, white gular region
Schulz 2013*		Former Yugoslavia, France, Bulgaria, southern Romania, Greece, Russia (Sochi)	
Cattaneo 2015	Images	Italy (Castelfusano, Castelporziano)	Same individuals from Cattaneo 1975, 2005
Speybroeck et al. 2016	Images	Bulgaria (Primorsko)	Dark grey colouration with black line in the temporal region, with a few normal yellow spots, white gular region
Glandt and Trapp 2021	Images	Montenegro	Dark grey colouration with black line in the temporal region, with a few normal yellow spots, white gular region
This study	Images	Italy (Lombardy)	Dark grey colouration with black line in the temporal region, with a few normal yellow spots, white gular region

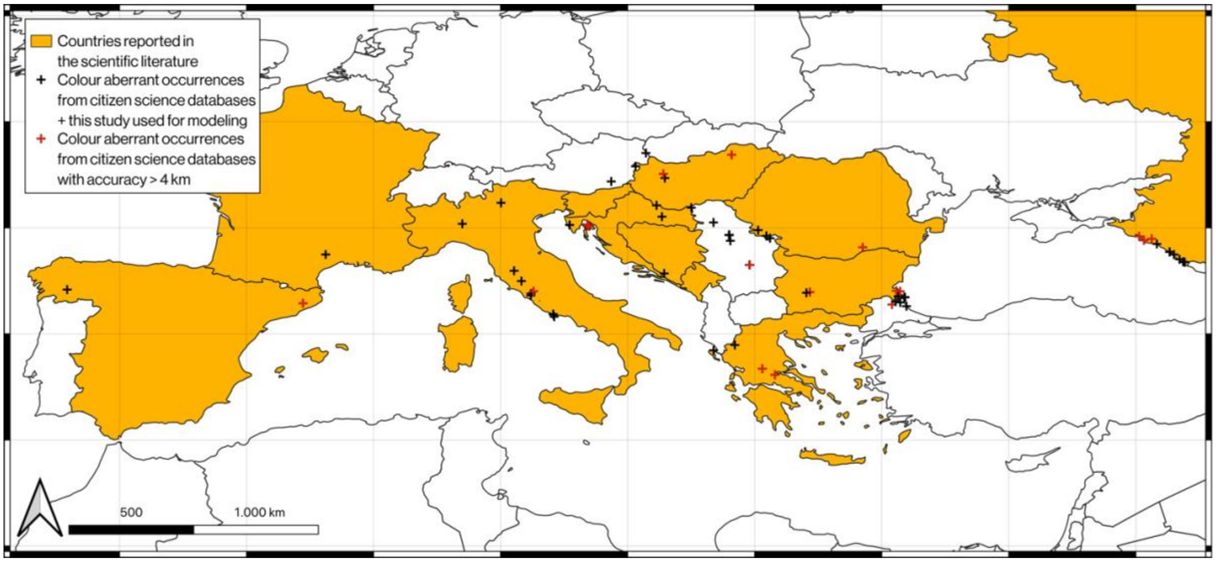

Figure 1. Map showing the countries for which the colour anomaly is reported in the scientific literature (orange) and the observations of colour aberrant individuals reported on citizen science databases and on this study (+; in black occurrences with accuracy < 4 km used for modelling, in red occurrences with accuracy > 4 km not included in the models).

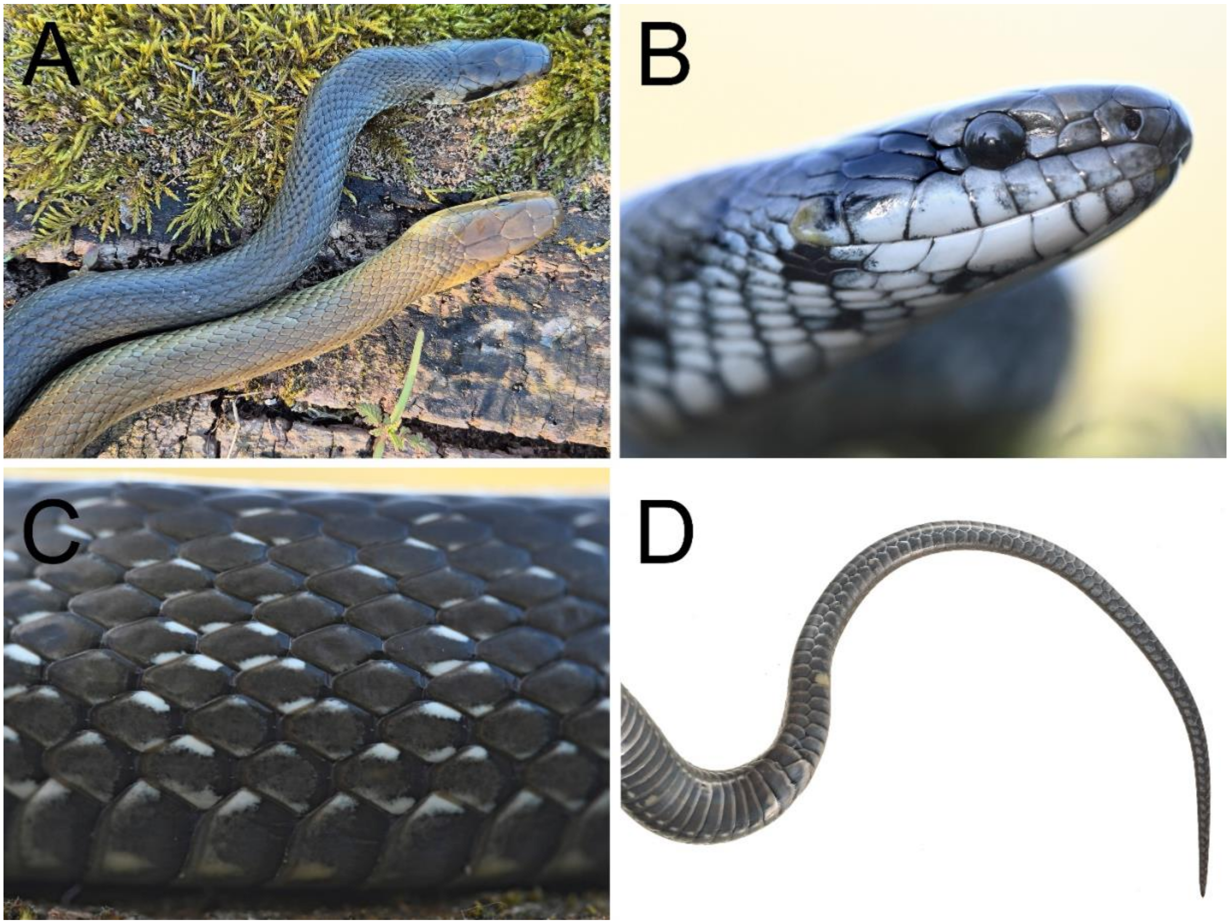

Figure 2. Dark-coloured adult female Aesculapian snake found near Pavia, Lombardy: comparison with a "typical" coloured adult individual found at the same site (A); lateral view of the head (B); detail of dorsal and ventral scales at mid-body (C); ventral view of the tail (D). Photocredit: Matteo R. Di Nicola.

Ecological niche modelling

The final ensemble model showed good statistical performance (mean AUC_{val} 0.84 ± 0.04, mean TSS_{val} 0.58 ± 0.08) and low overfitting (mean $AUC_{cal} - AUC_{val} = 0.05 \pm 0.06$). Variable permutation analysis indicated that mean diurnal temperature range (bio2) was the most important environmental predictor (0.63 ± 0.08), followed by mean annual temperature (bio1; 0.44 ± 0.07) and annual precipitations (bio12; 0.19 ± 0.21). The final ensemble model identified areas predicted as suitable for *Z. longissimus* with dark colour aberration using an average value that maximises the AUC (0.48) as the minimum suitability threshold (Fig. 3). The models predicted several areas as highly suitable across the known *Z. longissimus* range: parts of the Atlantic coast in Spain and France; the Tyrrhenian coast between France and Italy (including the inner portion of Liguria and Piedmont); the Adriatic coast of the Balkans countries from Croatia to northern Albania (including some northern islands and some Italian areas, i.e., the Po Delta valley and Gargano); and the Black Sea coasts of Russia, Georgia and Turkish Thrace. Several other suitable areas for this colour anomaly are also predicted across the species range (Fig. 3).

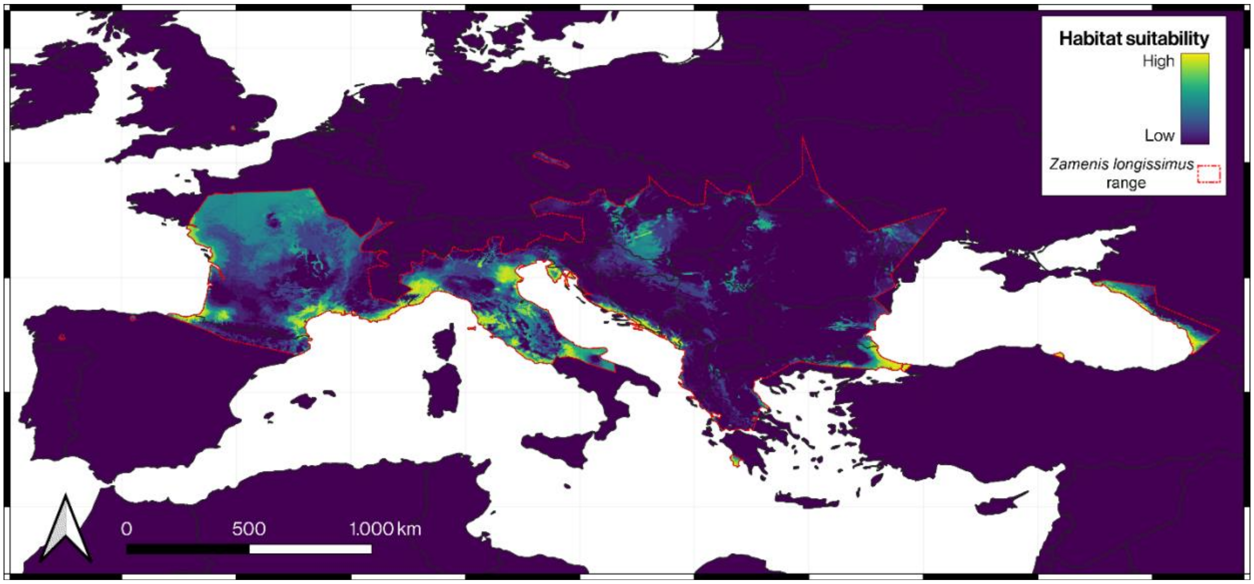

Figure 3. Habitat suitability map predicted by the ensemble models for dark coloured *Z. longissimus* tending to axanthism. Lighter colours indicate higher suitability while purple areas indicate areas under the minimum suitability threshold.

DISCUSSION

This study reports the first documented observation of a dark grey Aesculapian snake individual from Lombardy, Northern Italy. The individual exhibited a dark grey head with a distinct black spot in the temporal region and a ventral region transitioning from white under the head to black at mid-body, with few randomly distributed yellowish scales. Although rare, similar phenotypes have been reported throughout Europe and Asia Minor (Cattaneo 2015); however, the wide variability in colouration within this species complicates consistent categorisation of such anomalies.

The genetic background of melanism sensu lato has been tackled in several instances by zoologists, and a broad plethora of genetic variants has been found to induce skin darkening. Melanism has been associated with at least three genes in mammals and birds (Hadley 1997, Majerus 1998). The production of eumelanin is induced by the activation of Melanocortin 1 receptor (MC1R) by melanocortin hormones such as α-Melanocyte Stimulating Hormone (α-MSH).

The Agouti gene is involved in coat colouration in several mammal species, such as rats (Voisey and Van Daal 2002), by generating black hair with yellow subapical tips (Voisey and Van Daal 2002). The coat colour of agouti phenotypes is controlled by promoters which integrates with a single coding sequence (Voisey and Van Daal 2002). Furthermore, peptides derived from the proopiomelanocortin (POMC) prohormone are involved in numerous physiological processes, including stress response, anti-inflammatory response, sexual activity, energy homeostasis, and influence melanogenesis by activating MC1R (Roulin and Ducrest 2011).

In reptiles, however, evidence regarding molecular variants associated with this trait is vague and no gene has been confirmed to be directly linked with melanism. For example, the genetic background of melanism has been explored in multiple instances for the green whip snake *Hierophis viridiflavus*, a Mediterranean colubrid known for considerable variability in dorsal colouration, ranging from completely black to a pattern of yellow stripes over a dark background. Senczuk et al. (2021) and subsequently Meier et al. (2024) explored whether phenotypic variability could be explained by genetic variation via double-digest restriction-site associated DNA (ddRAD) genotyping; although polymorphic single-nucleotide polymorphisms (SNPs) correlated with melanism were identified, none involved coding regions explicitly implicated in melanogenesis. Thus, the matter remains unresolved.

Moreover, darker phenotypes are generally addressed with various terms, such as "melanic", "melanistic" or "axanthic", rendering the study of this topic both challenging and intriguing. For the target species of this study, such unusual darker phenotypes have been reported throughout its range (Fig. 1), encompassing different degrees of darkening and colour loss (Table 1). Some occurrences closely resemble our finding, showing a general darkening of skin and reduced yellowish colouration on both lateral and ventral surfaces. Thus, we defined the snake observed as chromatically aberrant, fitting closely what is commonly defined as “axanthic” rather than “melanic” or “melanistic” due to the presence of white pigmentation instead of yellow in the lower head, labial, and upper ventral region of the body.

We modelled the probability of detecting aberrant *Z. longissimus* across its range by implementing an ensemble model which predicted the most suitable areas based on climatic variables. Mean diurnal temperature range and mean annual temperature were the most important variables. Specifically, suitability was negatively associated with the former and positively associated with the latter. This evidence partially aligns with Gloger’s rule (Gloger 1833, Rensch 1929), which states that darker individuals are advantaged in hotter and wetter areas due to ultraviolet protection and camouflage (Delhey 2019). Furthermore, tyrosinase, a key enzyme in melanogenesis, is involved in immune processes in vertebrates; thus darker individuals might benefit from enhanced immune responses as a pleiotropic effect of tyrosinase in warmer, more humid contexts where pathogen proliferation is higher (Qiu et al. 2022).

Additionally, the areas of maximum suitability predicted by the model exhibit a Mediterranean climate shaped by higher average temperatures and lower diurnal ranges than continental climates, providing further support for this hypothesis.

Nevertheless, melanisation entails evolutionary costs. Darker animals may suffer increased predation risk due to enhanced visibility (Andrén and Nilson 1981) or incur higher energetic costs due to overexpression of melanin synthesis pathway (Roff and Fairbairn 2013). Consequently, dark phenotypes are maintained via a trade-off process between these energetic costs and the advantages of ultraviolet protection (such as increased fecundity and survival), resulting in their loss when selective pressures are not counterbalanced by adaptive advantages.

Although our findings align with the putative adaptive functions of darkening (Goldenberg et al. 2024), an alternative hypothesis must be acknowledged. The occurrence of aberrant darker phenotypes across the species' range could also result from neutral mutations arising randomly and producing abnormal phenotypes. From this perspective, darkening should be regarded as a neutral phenotypic variant neither strongly selected against nor providing substantial advantages. Additionally, if axanthism was indeed adaptive, one would expect higher frequencies of such phenotypes in environmental contexts where it is generally favoured by natural selection, which is not the case.

It must be noted that currently no gene is explicitly associated with axanthism. Only one case of moderate association has been found between this trait and the gene GTP cyclohydrolase II (gch2) for *Python regius* but the matter needs to be further developed and studied in detail (Garcia-Elfring et al. 2024). In this study, the axanthic phenotype is a result of a premature interruption of the codon in the previously cited gene resulting a defect in pterin pigments synthesis. Although there is little knowledge in gch2, it’s identified as a marker for xanthophores (Garcia-Elfring et al. 2024).

The findings of our investigation, which stemmed from an opportunistic encounter with an aberrant Aesculapian snake in Northern Italy, allowed to explore the bibliographic evidence for chromatic aberrations in this species and to provide preliminary information on the potential distribution of such phenotypes throughout Europe. However, molecular and histological studies are the necessary step for future investigations to unravel this matter and clarify the processes and mechanisms underlying the occurrence of axanthism in the species and whether they are applicable to a broader extent in other species showing aberrant colourations.

Lastly, it is important to highlight that our model was computed using a limited number of occurrences across the entire known distribution of *Z. longissimus*, and was therefore trained exclusively on the available records. As a result, it is highly conservative, predicting large areas below the minimum suitability threshold. Given the small dataset and low average coordinate accuracy, fine-scale modelling was not feasible. Accordingly, our results should be interpreted as indicative of potential areas where aberrant *Z. longissimus* might occur, warranting further field validation. Nevertheless, the approach showed good statistical performance, and its predictions were considered reliable. In fact, most areas identified as highly or moderately suitable corresponded to confirmed records from scientific literature or citizen science (see Fig. 1). After our analyses had been completed, two further unpublished observations of axanthic-like *Z. longissimus* from the Tuscan coast (Scarlino and Montioni Natural Park; G. Radi, pers. comm.) came to our attention. These observations provide additional support for our model, which predicted high suitability in that area despite being trained without local records.

ACKNOWLEDGEMENTS

The authors thank Giacomo Radi for sharing information on two unpublished records, corroborated by photographic evidence. The temporary capture of snakes was carried out following permits: MASE/Ministero dell'Ambiente e della Sicurezza Energetica (MASE N. 0073290.18-04-2024), approved by ISPRA (Protocol N. 0066053.08-04-2024).

AUTHOR CONTRIBUTIONS

Conceptualisation: L.C., F.S., and M.R.D.N.; Data curation: L.C.; Formal analysis: L.C.; Investigation: L.C., I.D.H.K, and M.R.D.N.; Methodology: L.C., and M.R.D.N.; Supervision:

F.S., and M.R.D.N.; Visualisation: L.C., and M.R.D.N.; Writing – original draft: L.C., I.D.H.K., F.S., and M.R.D.N.; Writing – review and editing: L.C., F.S., and M.R.D.N..

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Submitted: 7 August 2025

First decision: 27 August 2025

Accepted: 29 August 2025

Edited by Francesco Paolo Faraone