A SUBSTRATE-DRIVEN PLASTICITY HYPOTHESIS FOR THE MONTEREY ENSATINA SALAMANDER (*Ensatina eschscholtzii*)

Nasri Ahmed Rami

Independent researcher

Corresponding author, e-mail: raminasri151@gmail.com

***Abstract.*—Phenotypic plasticity allows many amphibians, including several salamander species, to adjust skin luminance in response to background brightness. In habitats with heterogeneous substrates in color and brightness, such plasticity may generate substantial individual variation within a population. In a population of the terrestrial salamander *Ensatina eschscholtzii*, a recent study documented an unusually high frequency of atypical light phenotypes characterized by pink and orange dorsal coloration. This population occurs in a site dominated by extensive light-colored dune sand, suggesting a potential environmental influence on apparent coloration. We propose that substrate-driven plasticity may shift the apparent luminance of typical individuals toward lighter phenotypes in this species, and predict that this response occurs primarily in juveniles and diminishes through ontogeny.**

Key Words.—Amphibian coloration; background matching; color change; phenotypic plasticity; Terrestrial salamander.

Ensatina eschscholtzii is a plethodontid salamander that comprises a series of geographically differentiated populations forming a ring around California's Central Valley, representing a classic example of a ring species complex in western North America (Stebbins 1949; Wake 1997). Within this system, the Monterey population displays relatively uniform dorsal coloration, ranging from pinkish-brown to reddish-brown (Stebbins and McGinnis 2018), and is hypothesized to rely on dorsal coloration to achieve predator avoidance through background-matching crypsis (Stebbins 1949; Kuchta 2005).

Background matching is one of the primary anti-predator strategies in amphibians (Rudh and Qvarnström 2013), and its effectiveness is influenced by the luminance of the surrounding substrate (Barnett et al. 2020; Caro and Koneru 2021). When substrate luminance changes, many amphibian species can adjust the luminance of their skin through phenotypic plasticity, allowing their coloration to better match the background and maintain camouflage (Duarte et al. 2017; Liedtke et al. 2023; Zhai et al. 2024; Lorrain-Soligon et al. 2025). This plasticity is mediated by specialized cells arranged in layers within the dermis called chromatophores, which collectively determine skin color in amphibians, allowing individuals to better match their background (Bagnara et al. 1968; Nilsson Sköld et al. 2013; Zhai et al. 2024). In some amphibian species, these processes can produce substantial luminance changes, from light to very dark coloration in response to background brightness (Choi and Jang 2014; Liedtke et al. 2023; Zhai et al. 2024). This type of color plasticity has been linked to intraspecific variation in dorsal coloration in many amphibian taxa (Kang et al. 2016; Preißler et al. 2021; Lorrain-Soligon et al. 2025).

Substrate-driven color plasticity has been documented in several salamanders, though most evidence comes from larval stages (Garcia and Sih 2003; Segev 2009; Polo-Cavia and Gomez-Mestre 2017). However, in the tiger salamander *Ambystoma tigrinum nebulosum*, substrate-induced plasticity persisted after metamorphosis but it was slower and expressed within a narrower range in older individuals (≥3 years; about 30 to 50 days to shift color) (Fernandez and Collins 1988). Kraemer et al. (2012) found that *Plethodon cinereus*, a plethodontid salamander relative of *Ensatina eschscholtzii*, exhibits long-term color change when maintained under dark captive conditions. Whether *Ensatina eschscholtzii* possesses this plasticity remains untested (Rich et al. 2021).

Rich et al. (2021) documented an atypically elevated frequency of light-colored individuals in the *Ensatina eschscholtzii* population at Fort Ord UC Reserve (Monterey County, California), a heterogeneous habitat where light-colored dune sand represents a significant component of the landscape. They identified two light morphs, out of an otherwise dark brown population, from photographs by visual scoring: pink (11%), classified as leucistic, and orange (28%), classified as xanthistic. Both leucism and xanthism are pigmentation abnormalities; leucism produces pale or pinkish appearance (Gould 2025), whereas xanthism is defined by the predominance of yellow or orange hues (Allain and Goodman 2017; Pedroso-Santos et al. 2022). However, both leucism and xanthism are rare in natural amphibian populations and are occasionally reported as isolated individuals, often after decades of field surveys (Allain and Goodman 2017; Lunghi et al. 2017; Pedroso-Santos et al. 2022; Capula et al. 2023; Parayko et al. 2023). The origins of these phenotypes remain unclear and are generally attributed to genetic mutations or environmental influences (Camacho et al. 2022; Parayko et al. 2023). Although Rich et al. (2021) suggested relaxed predation as a possible explanation for this pattern, they also proposed short term background matching plasticity as a potential confounding factor for brown-colored individuals, they argued that leucistic and xanthistic morphs were not expected to exhibit this plasticity due to their lack of melanin pigments. The normal coloration of *Ensatina eschscholtzii* in Monterey populations ranges from pinkish-brown to reddish-brown (Stebbins and McGinnis 2018). If this species is capable of substrate-driven luminance plasticity, light substrates could shift the appearance of normal pinkish-brown and reddish-brown phenotypes toward lighter pink and orange tones, potentially producing the morphs scored as leucistic or xanthistic in photographic surveys.

Figure 1. Representative pigmentation variation in the Monterey Ensatina population. Panels A–D show pale phenotypes, E–I orange phenotypes, and J–L darker phenotypes. All photographs sourced from https://www.inaturalist.org [Accessed 22 April 2026] under CC BY-NC licenses. (Photographed by William Mason [A, C, D]; Kuoni W [B, F]; Diego Balbuena [E]; Yinan Li [G, I]; Oonagh Degenhardt [H]; Theresa Wood [J]; Brandon Troth [K]; Rosescribe [L].)

Figure 1 illustrates broad continuous variation in dorsal coloration among individuals, ranging from pale pink and orange to near black, with numerous intermediate forms. While some pale specimens resemble leucistic or xanthistic phenotypes, the absence of distinct color boundaries in the sampled images indicates continuous variation rather than discrete genetic morphs.

The variation between pale pink, orange, and brown appears to differ primarily in brightness, aligning with patterns expected under substrate-driven plasticity (Preißler et al. 2021; Liedtke et al. 2023; Zhai et al. 2024). We therefore hypothesize that *Ensatina eschscholtzii* possesses substrate-driven brightness plasticity, and that the unusually high frequency of light-colored individuals at Fort Ord reflects environmentally induced luminance shifts rather than genetic pigmentation abnormalities. We further predict that this plastic response is strongest in juveniles and becomes progressively slower and more constrained with ontogeny.

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