



Transient Albinism in the Streamside Salamander (*Ambystoma barbouri*) with a Review of Color Abnormalities in *Ambystoma*

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Herpetologists have long been fascinated by the color patterns of reptiles and amphibians, and coloration has been shown to influence reproductive success, behavior, and survival across taxa (Protas and Patel 2008; Olsson et al. 2013). For example, Hegna et al. (2013) found that within a species of poison frog (Oophaga pumilio) predation levels were higher on a green morph than on either the cryptic or conspicuous red morph. Additionally, evidence indicates that polymorphism within species is associated with important behavioral traits. Reiter et al. (2014) described differences in levels of aggression between striped and unstriped color polymorphs of the Red-backed Salamander (Plethodon cinereus); striped salamanders were more aggressive and territorial than unstriped individuals, which might explain the former's ability to mate with larger, presumably more fecund females. Such findings indicate that coloration can have significant effects on the ecology and persistence of species and is therefore worthy of attention.

In addition to typical variations in patterning (i.e., "wildtype" polymorphisms), atypical colorations that are less frequently observed in nature range from true albinism (i.e., a total lack of melanin) to melanism with various intermediate levels of pigment expression (Henle et al. 2017a). Such oddities may be linked to genetic mutations that cause a reduction or lack of pigment-storing cells (i.e., chromatophores), the inability to produce particular pigments (e.g. melanin), or the over-production of pigments leading to unusually dark or colorful individuals (Nachman et al. 2003; Kamaraj and Purohit 2014). Some forms of coloration (i.e., albinism, leucism) are rarely seen in nature, possibly due to increased predation or disease (e.g., skin cancer) and potential for genetically-linked mutations (Childs 1953; Krecsák 2008; Szydłowski et al. 2020). Yet, in some instances abnormal coloration could be adaptive. For example, reduced pigmentation is common in low-light ecosystems like caves where lack of pigment is not detrimental (Protas et al. 2006; Soares and Niemiller 2020).

Albinism is of particular biological importance because it results in a total lack of melanin, which in most cases would make individuals more conspicuous and likely to become prey or could eliminate protection from ultra-violet light. Frequencies of albinism vary across taxa. For example, a review by McCardle (2012) indicated that birds and mammals have the highest number of species with albinism; however, reptilian and amphibian color morphs are sporadically recorded in natural populations, particularly in salamanders (Henle et al. 2017b). Given that rates of taxonomic bias are high, reports of albinism of ectothermic vertebrates might be low due to underreporting or an unconscious bias in the publication process (Bonnet et. al. 2002). Consequently, reporting atypical coloration in lesser-studied taxa (e.g., salamanders) is important, as are occasional syntheses of existing knowledge (e.g., literature reviews) to bolster research and encourage future reporting.

Albinism usually is caused by a mutation in genes involved in the synthesis of melanin. Because this biochemical pathway has multiple steps, several potential mutations can result in albinism (Bian et al. 2021). For example, the Black-spotted Frog (Pelophylax nigromaculatus) has at least five different recessive mutations that can result in albinism (Nishioka and Ueda 1985; Nishioka et al. 1987). Furthermore, subcategories or special cases of albinism can result in considerable variation in how albinism is expressed. For example, in mammals, albinism can result in a lack of pigment in the eyes, skin, and hair (oculocutanesous albinism) or only the eyes (ocular albinism) (Montoliu et al. 2014). In amphibians and reptiles, individuals may be full or partial albinos if all or some tissues lack melanin, respectively (Henle et al. 2017b). Also important is noting that amphibians and reptiles have multiple types of pigment-producing cells (i.e., chromatophores), including melanophores that store melanin, xanthophores/erythrophores that store yellow, orange, or red pigments, and iridophores that store light-scattering,

iridescent compounds. Therefore, the amount of melanin is only one factor determining coloration, and conditions other than albinism can result in a pale or white appearance. This is well-illustrated in the Axolotl (Ambystoma mexicanum), which has an albino form that lacks all melanin but also a white or leucistic form that appears pale due to the absence of all chromatophores in the skin (Houillon and Bagnara 1996). Thus, an albino Axolotl can still express pigments in xanthophores and iridophores, which gives it a yellowish hue, but its melanophores are devoid of melanin. The leucistic form, however, expresses no skin pigment, not because it cannot produce pigments, but because the chromatophores are absent. Therefore, leucistic individuals appear white due to a total lack of pigment, but their eyes are dark because the ocular pigments do not depend on chromatophores. As such, leucistic and albino conditions are often confused in the literature (Henle et al. 2017a).

An interesting but little studied case of albinism is transient albinism, which is the condition in which individuals lack melanin as embryos but exhibit normal coloration later in life (Henle et al. 2017a). Transient albinism can occur when females are incapable of producing melanin during oogenesis, but offspring genes allow for melanin production later. This is the expected condition when an albino female mates with a wild-type male, producing heterozygous offspring capable of melanin production. The melanin initially present in amphibian eggs is maternally-derived in the ovary and functions as part of a suite of strategies to protect embryos from harmful ultra-violet radiation (UVB) (Licht and Grant 1997). This melanin is stored in egg organelles known as melanosomes that are concentrated on the upper, dorsal (or animal pole) portion of the embryo. As such, species that nest in cryptic sites (e.g., under rocks) usually lay eggs that lack melanin, whereas those that oviposit in areas exposed to sunlight lay eggs heavily pigmented with melanin (reproductive modes 1 versus 2; Salthe 1969). Therefore, transient albinism refers specifically to eggs that are laid without melanin by a species that typically lays melanin-rich eggs (Henle et al. 2017a.). To illustrate, consider that salamanders of the genus Eurycea naturally lay white eggs that lack melanin, and this would therefore not be considered a case of transient albinism. Species in the genus Ambystoma, however, lay melanin-rich eggs and transient albinism can occur in these species. For example, Harsa-King (1980) demonstrated that, although albino Axolotls can create melanosomes during oogenesis, these organelles are never filled with melanin; therefore, albino females lay white eggs devoid of pigment. Wild-type or white (leucistic) Axolotls, however, lay eggs darkly colored with melanin (Houillon and Bagnara 1996). Thus, when an albino female mates with a leucistic or wild-type male, the eggs are initially white, but the embryos eventually produce their own melanin. In the case of leucism, melanin is present only in the embryo's eyes. Transient albinism also can be induced in a laboratory for research purposes via the application of chemicals, most commonly phenylthiocarbamide (PTC), which inhibits melanin production (Piatt 1951; Dumont and Eppig 1971; Camp and Lardelli 2001). This procedure allows for the study of embryonic melanin production in species in which maternal and embryonic melanin are indistinguishable. For example, Piatt (1966) used a clutch of transient albino Spotted Salamanders (A. *maculatum*) to study the production of melanin in the developing eye. In typical embryos, distinguishing between retinal pigment produced by the female versus the developing offspring would be difficult.

Among amphibians, transient albinism has been observed in species including the Moor Frog (Rana arvalis), European Green Frog (Bufotes viridis), Spotted Salamander (A. maculatum), and the Common Parsley Frog (Elodytes punctatus) (Piatt 1966; Rivera et al. 2001; Henle et al. 2017b.; Kaczmarski 2018), although records are generally rare (Henle et al. 2017b). Herein we describe a novel incidence of transient albinism in the Streamside Salamander (Ambystoma barbouri). Although albinism has been reported for A. barbouri (Petranka 1998), to our knowledge, this is the first report of transient albinism in the species and the first report of albinism of any kind in Tennessee, where populations are threatened by habitat destruction and reproductive isolation. In addition to this novel report, we present a comprehensive review of abnormal color variations in Ambystoma to place our finding within the broader context of aberrant coloration in the genus and provide a useful tool for future researchers who wish to study color aberrations in Ambystoma.

Methods

Observation of transient albinism.-We discovered two nests with white embryos (i.e., transient albinos) while searching for A. barbouri eggs to use in an incubation study. To conduct nest surveys, we selected a location in a stream and walked upstream, turning every rock that was large enough for nesting to occur, and returning rocks to their original position. We initially assumed these white eggs were dead embryos as dead eggs often are invaded by fungi and appear discolored, but on further examination with a jeweler's loupe, cell division was visible and no fungal hyphae were present. We photographed each nest and completed egg counts using imageJ software (National Institute for Health: https://imagej.net/ ij/index.html). We collected eight transient albino eggs and returned them to the laboratory to incubate at 10 °C and 20 °C (n = 4 per temperature). These temperatures were selected for convenience, as we were conducting a study of the effects of incubation temperature on development using 5, 10, 20, and 25 °C treatments. We selected the two intermediate temperatures to increase the likelihood of successful development (Garcia et al. 2003). Once hatched, larvae were maintained

individually inside 9 x 3 in PVC tubes kept in a 20-gallon tank and fed brine shrimp hatchlings and frozen bloodworms three times a week until metamorphosis. We housed metamorphs individually in Sterilite containers ($11 \times 6.6 \times 2.7$ in) with dechlorinated water, paper towels, and damp cardboard, and fed them Dwarf White Isopods (*Trichorhina tomentosa*) and European Nightcrawlers (*Dendrobaena hortensis*). Individuals were photographed and massed at metamorphosis and every thirty days thereafter.

Literature Review.—We conducted a systematic literature review using GoogleScholar and the Tennessee Technological University library search engine (EagleSearch: https://www. tntech.edu/library/) using the search terms Ambystoma, Caudata, salamander AND albinism, coloration, leucism, melanism, and variation. We also utilized EndNote to locate "Notes" published in Herpetological Review prior to 2019 that otherwise do not appear in search engine results. We reviewed "Herpetoculture" and "Natural History Notes" sections in Herpetological Review published after 2019. We also collected records from Dyrkacz (1981), who previously reviewed albinism in reptiles and amphibians and reported records that were otherwise unpublished. We reviewed articles for reports of any color abnormalities in the genus Ambystoma from all years until March 2023. For each article, we reviewed the literature cited for additional records. Studies included in this review had to be published or translated into English and report a sighting of one or more individuals in nature with at least one abnormal color variation. If the origin of the individuals was unknown (e.g., Piatt 1966), we did not include the record in our review. We defined abnormal color variations as albinism, leucism, hypomelanism, melanism, and partial melanism or albinism; all other variations were excluded. We used Henle et al. (2017a), a commentated glossary of color anomalies, to define these colorations: albino = lacking all melanin, including the eyes (including transient albinism); leucistic = lacking all exterior pigment, excluding the eyes; hypomelanism = substantial reduction in pigment; melanism = completely black body; partial melanism = only part of the body displays typical pigmentation, the rest displays melanism; partial albinism = only part of the body displays typical pigmentation, the rest lacks melanin.

Results

Observation of transient albinism in Ambystoma barbouri.— On 9 December 2022, in the Central Basin of Tennessee (Sumner County), we found white embryos comingled with typical black embryos. One nest contained 85 typical and 110 transient albino embryos and the other contained 223 typical and 104 transient albino embryos (Fig. 1). The four eggs incubated at 20 °C died but three embryos in the 10 °C incubator continued developing. The embryos remained albino through the formation of the tailbud and gill plate



Figure 1. Two Streamside Salamander (*Ambystoma barbouri*) nests in the Central Basin of Tennessee with both normal and transient albino eggs. Photographs by Joshua Hall (left) and Julia Thulander (right).

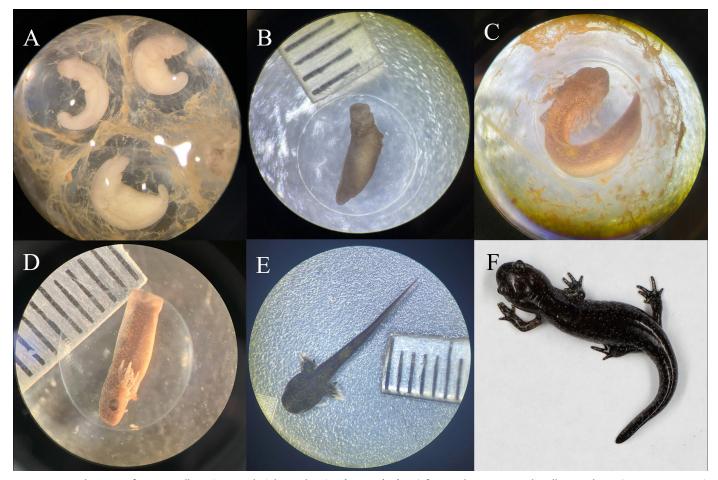


Figure 2. Development of transient albino Streamside Salamanders (*Ambystoma barbouri*) from embryos to juvenile: Albino embryos (Harrison stage 30) (A), typical embryo (Harrison Stage 36) (B), development of chromatophores of transient albino embryo (Harrison stage 39) (C), typical embryo (Harrison stage 39) (D), newly hatched transient albino larvae (E), and transient albino metamorph with normal coloration (F). Photographs by Joshua Hall (A) and Julia Thulander (B–F).

(i.e., Harrison stages 26–29); however, once limb buds began forming, chromatophores became visible, and the embryos expressed dark pigment (likely, melanin; Fig. 2). At hatching, the two remaining larvae had typical coloration and continued to present coloration consistent with other *A. barbouri* (Fig. 2). This phenomenon was termed transient albinism by Henle et al. (2017b) and, to our knowledge, this is the first published observation in *A. barbouri*; however, transient albinism has been recorded for the Small-mouthed Salamander (*A. texanum*), which is the sister species to *A. barbouri* (Cahn 1930).

Abnormal coloration in Ambystoma.—Of the 32 currently recognized species of Ambystoma (AmphibiaWeb), abnormal color patterns in wild animals have been observed in ten (31.3%), with a frequency of occurrence higher in some than others (Table 1). The species most commonly identified with abnormal coloration are A. maculatum (Spotted Salamander) and A. opacum (Marbled Salamander) (Table 1; Fig. 3). Complete albinism is the most commonly recorded abnormal coloration and has been found in eight of ten spe-

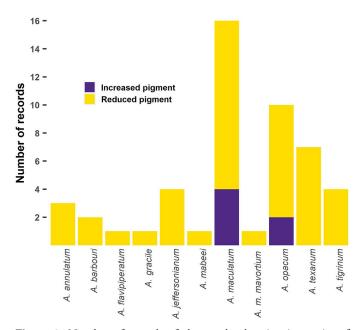


Figure 3. Number of records of abnormal coloration in species of *Ambystoma* showing reductions or increases in pigment.

Table 1. Records that report wild-caught *Ambystoma* with color aberrations. Studies are listed alphabetically by species. If multiple records exist, they are reported alphabetically by the last name of the first author. "NA" indicates that a number of individuals was not reported or that a specific location was not provided. "Albino" refers to complete albinism unless otherwise noted. Color morphs represent our designation based on Henle et al. (2017a) and might differ from the term used by the original author.

Species	Source	Number	Life Stage	Color Morph	Location
A. annulatum	Trauth and Cartwright 1989	1	Larva	Albino	Baxter County, Arkansas
	Anderson 2020	1	Larva	Leucistic	Pulaski County, Missouri
	Anderson 2020	1	Larva	Leucistic	Warren County, Missouri
A. barbouri	Petranka 1998	1	Adult	Albino	Fayette County, Kentucky
	Thulander and Hall 2023	214	Eggs	Albino (transient)	Sumner County, Tennessee
A. flavipiperatum	Cortés-Vázquez et al. 2016	1	Juvenile	Leucistic	Tecolotlán, Mexico
A. gracile	Dyrkacz 1981	1	Adult	Albino	Multhomah County, Oregon
A. jeffersonianum	Collins, J.T. 1965	1	Adult	Albino	Hamilton County, Ohio
	Dyrkacz 1981	1	Adult	Albino	Hamilton County, Ohio
	Dyrkacz 1981	7	Larva	Albino	Hamilton County, Ohio
	Harris 1967	18	Larva	Albino	Washington County, Maryland
A. mabeei	Palis et al. 2020	1	Larva	Hypomelanisitc	Berkeley County, South Carolina
A. maculatum	Bieri 2021	4	Adult	Albino	Marquette County, Michigan
	Bieri 2021	NA	Eggs	Albino	Marquette County, Michigan
	Bogart et al. 2017	2	Adult	Melanistic	Ontario, Canada
	Brandt 1952	1	Adult	Albino	Washington County, Tennessee
	Britcher 1898	NA	Eggs	Albino (transient)	NA
	Dyrkacz 1981	1	NA	Leucistic	Campbell County, Kentucky
	Dyrkacz 1981	1	Adult	Albino	Cecil County, Maryland
	Dyrkacz 1981	1	Adult	Albino	Thompkins County, New York
	Easterla 1968	2	Adult	Melanistic (1 partial)	Clay County, Arkansas
	Hartzell 2020	1	Juvenile	Hypomelanistic	Montour County, Pennsylvania
	Hensley 1959	1	Adult	Albino	Prince Georges County, Maryland
	Lowcock 1985	1	Adult	Albino	Oak Bay, Quebec, Canada
	Rye 1991	1	Adult	Albino	Oak Bay, Quebec, Canada Ontario, Canada
	Smith and Michener 1962	1	Adult	Albino	Thompkins County, New York
	White 2002	1	Adult	Partially melanistic	Fairfax County, Virginia
	White 2002	1	Adult	Melanistic	Fairfax County, Virginia
	Blais and Sprague 2020	2	Larvae	Hypomelanistic	Yavapai County, Arizona
A. opacum	Campbell 2011	1	Adult	Albino	Franklin County, Tennessee
	Deegan et al. 1998	3	Larva	Albino	Newport County, Rhode Island
	Dyrkacz 1981	3	Larva	Albino	Baltimore County, Maryland
	Dyrkacz 1981	8	Larvae	Albino	Noxubee County, Mississippi
	Hall 2020	1	Adult	Melanistic	Weakly County, Tennessee
	Mitchell and Church 2002	1	Larva	Leucistic	Caroline County, Virginia
	Mitchell and Church 2002	1	Metamorph	Leucistic	Caroline County, Virginia
	Simpson and Wilson 2010	4	Adult	Melanistic (1 hypomelanistic)	Hamilton County, Tennessee
	Waltson and Register 2004	1	Adult	Partial albino	Alexander County, Illinois
	Waltson and Register 2004	3	Larva	Partial albino	Alexander County, Illinois
A. texanum	Allyn and Shockley 1939	1	Adult	Albino	Vigo County, Indiana
	Cahn 1930	NA	Eggs	Albino (transient)	Champaign County, Illinois
	Dyrkacz 1981	2	Adult	Leucistic	Stoddard County, Missouri
	Jones 1991	2	Adult	Albino	Oklahoma County, Oklahoma
	Underhill 1968	NA	Eggs	Albino (transient)	Champaign County, Illinois
	Underhill 1968	NA	Larva	Albino (transient)	Champaign County, Illinois
	Underhill 1968	1	Adult	Albino	Champaign County, Illinois
A. tigrinum	Childs and Howard 1955	NA	Larva	Albino	Madera County, California
	Dyrkacz 1981	1	Juvenile	Albino	Kennedy County, Colorado
	Dyrkacz 1981	1	Larva	Albino	Boulder County, Colorado
	Humphrey 1967	1	Metamorph	Albino	Kandiyohi County, Minnesota

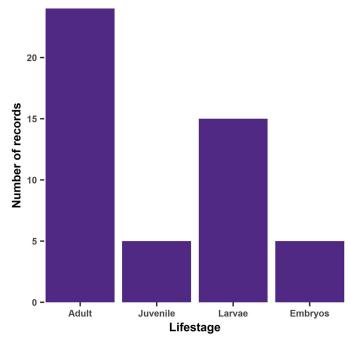


Figure 4. Number of publication records of abnormal coloration in *Ambystoma* according to life stage.

cies that exhibited color aberrations (Fig. 3). Of the records, 24 reported sightings of adults (50% of records), whereas five reported sightings in juveniles, 15 in larvae, and five in embryos (Fig. 4).

Discussion

During oogenesis, female Ambystoma deposit melanosomes filled with melanin inside each egg, which serve to protect embryos from UVB damage (Harsa-King 1980). This pigment provides the embryo with its initial coloration; however, later in development, at approximately Harrison stage 35, chromatophores become visible and the developing offspring begins producing pigment usings its own genome (Wallace and Selman 1990; Thibaudeau and Altig 2012). For context, this developmental stage corresponds with the appearance of gill buds and first beating of the heart (Bordzilovskaya and Dettlaff 1979). Therefore, transient albinism in Ambystoma would manifest as embryos that are white until the point of gill formation, which is consistent with our observations. Thus, we report a novel finding of transient albinism in A. barbouri, having found two nests partially with eggs that presented as complete albino, of which two surviving embryos from eight eggs acquired normal pigmentation over time (Fig. 2). Transient albinism is rarely described in nature, potentially because eggs containing albino embryos are presumed dead and not examined further. Moreover, little opportunity exists for observing transient albinism compared to total albinism given that the more conspicuous life stages (larvae, adults) no longer express the trait.

We believe the most likely explanation for our observation is that a single albino female produced all the transient albino eggs we discovered and that surviving embryos from our study are heterozygous for albinism. This is plausible given that albinism has been observed before for A. barbouri, its sister species A. texanum, as well as a variety of other species of Ambystoma. Although the nests we discovered contained wild-type eggs, these were likely from a different female. Streamside Salamanders will often spread a clutch of eggs across multiple nest sites resulting in several females ovipositing on the same rock (Niemiller and Reynolds 2011). Moreover, A. barbouri in Tennessee can produce clutch sizes of 98-278 eggs (Niemiller et al. 2009) and the total number of transient albino eggs discovered (214) is within this range. A single female could not have laid all the eggs, including the wild-type eggs (n = 522). Therefore, the alternative explanation is that two females each produced both albino and wild-type eggs. This is theoretically possible. Houillon and Bagnara (1996) conducted embryonic tissue transplant experiments among white, albino, and wild-type axolotls some of which resulted in females capable of producing both normal and albino eggs. Their experiments demonstrated the endogenous production of oocyte melanin by the ovary. Therefore, a phenotypically wild-type female could produce albino eggs if the tissue of the ovary is albino, perhaps resulting from a mutation early in development in the gonadal cell lineage. However, the rule of parsimony leads us to believe that genes for albinism exist in A. barbouri populations at very low frequency and occasional albino females survive to reproduce. This is in our opinion the most likely explanation.

In our literature review, the most reports of abnormal coloration were in A. maculatum and A. opacum, but they also have some of the largest ranges within the genus (Petranka 1998) thus providing more opportunities for occurrences to be discovered. Indeed, a positive relationship exists between a species' range and the reporting of trait data for that species (Etard et al. 2020). Alternatively, the Blue-Spotted Salamander (A. laterale) and Tiger Salamander (A. tigrinum) have similarly large ranges but have far fewer records (Table 1), which leads to multiple conclusions. Compared with other species, color abnormalities may be less common in some species because abnormally colored individuals are quickly removed by predators, they possess low levels of genes that lead to color abnormalities, or detection probability is lower because they are less studied or because they utilize more cryptic nesting habitat.

Additionally, A. maculatum and A. opacum have been studied extensively in their natural habitats whereas other species (e.g., A. barbouri, A. mexicanum, and A. annulatum) are less studied in their habitats. Such work considers ecology, evolution, toxicology, and population dynamics and could result in more opportunities to detect color abnormali-

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ties for A. maculatum and A. opacum. The location of records should also be considered as they usually do not come from across the entire range of any species, indicating that some populations have a greater number of carriers for abnormal coloration genes. Alternatively, those populations are more heavily studied or commonly observed. The latter is a likely explanation. For example, albinism appears to be more common in the northern range of the Common Garter Snake (Thamnophis sirtalis) compared with the southern range; however, Stephenson and Drace (2014) showed that when compared with records of wild-type individuals, no difference in the incidence of albinism exists across latitude. Ambystoma maculatum and A. opacum are also the only species with reported melanistic individuals, possibly indicating a higher frequency of carriers for albinism and melanism in these species. A general trend across the genus of more albinos than melanistic individuals reported is common in other amphibian genera (Jablonski et al. 2014). Also worth noting is that for some species detection of melanistic individuals may be difficult due to normal dark coloration (e.g., A. barbouri, A. jeffersonianum, and A. talpoideum). Moreover, some of these species have relatively high variation in typical coloration, which could reduce the probability of reporting as some researchers might assume that melanistic individuals are within the typical range of colors, whereas species like A. opacum and A. maculatum have conspicuous patterns that facilitate recognition of melanistic individuals.

In addition to variation across species, we observed differences in color aberrations across life stages. If conditions like albinism impart a survival disadvantage, the null expectation is that the greatest number of reports would be for eggs and that the number of aberrant individuals would decrease with each life stage — but this is not what we observed. Some life stages might be more vulnerable to predation due to color variants than others. For example, eggs, juveniles, and adults could occupy more cryptic habitat than larvae, which are often in the open water column rather than concealed beneath rocks or soil (Duellman and Trueb 1994). Indeed, the highest number of aberrant coloration reports are for adults and this likely is attributable to the life history of Ambystoma. Adults spend much of the year underground protected from visual predators and emerge only for short periods of time for nocturnal breeding events. Therefore, traits like albinism could be less detrimental to adult survival than in other life stages that remain above ground (e.g., dispersing metamorphs, larvae). Albino Ambystoma might be most vulnerable to predation in the egg and larval stages. Alternatively, differences in records across life stages might merely reflect the relative ease of observing adults in comparison to younger life stages (i.e., detection probability). For example, adults of some species are highly conspicuous in coloration, but their larvae are relatively difficult to identify, even for trained researchers. Thus, an abnormally pigmented adult would be more easily recognized than a larva. Moreover, adults are often the focus of monitoring efforts and population studies (e.g., capturemark-recapture) potentially resulting in greater detection probability of aberrantly colored adults compared with other life stages.

Although color abnormalities are fascinating due to their rarity, they are difficult to study. The Axolotl (A. mexica*num*) is an exception and has been used at length to understand color polymorphism and has been genetically altered or bred to create a wide variety of color morphologies (Frost and Malacinski 1980; Frost-Mason and Mason 1996). These color morphs are often used in research. Interestingly, the genes for albinism were introduced to A. mexicanum through somatic cell nuclear transfer with an albino A. tigrinum although, to our knowledge, albinism has not been formally reported in a wild-caught Axolotl, though albinos are common in the pet trade (Humphrey 1967). Although hybridization experiments between A. mexicanum and A. tigrinum were unsuccessful, natural hybridization among other species of Ambystoma is possible, leading to the possibility for gene transfers, which could be used to understand genetic links between such abnormalities and other genetic mutations (Riley et al. 2003). For example, albinism is present in both A. barbouri and A. texanum, which are sister species, and could have resulted from a natural hybridization event given that such hybridization is common (Niedzwiecki 2005).

In conclusion, we report the first instance of transient albinism in the Streamside Salamander (*A. barbouri*) and provide a review of color aberrations in *Ambystoma*. Our review shows that abnormal coloration is well-documented in some species (e.g., *A. maculatum* and *A. opacum*) but not others, likely due to a variety of factors including variation in range, robustness of populations, and availability of populations for study. As genomic tools become more readily available (and cost effective), important future work should analyze the genetic underpinnings of these abnormal colorations and make comparisons across species and populations with the goal of understanding the evolutionary and ecological significance of coloration. We believe the genus *Ambystoma* would be a prime candidate for such research.

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Literature Cited

- Allyn, W.P. and C. Shockley. 1939. A preliminary survey of the surviving species of Caudata of Vigo County and vicinity. *Proceedings of the Indiana Academy* of Science 48: 238–243.
- AmphibiaWeb: Information on Amphibian Biology and Conservation. 2023. AmphibiaWeb, Berkeley, California, USA. https://amphibiaweb.org/>.
- Anderson, T. 2020. Ambystoma annulatium (Ringed Salamander). Development. Herpetological Review 51: 525–526.
- Bian, C., R. Li, Z. Wen, W. Ge, and Q. Shi. 2021. Phylogenetic analysis of core melanin synthesis genes provides novel insights into the molecular basis of albinism in fish. *Frontiers in Genetics* https://doi.org/10.3389/ fgene.2021.707228.
- Bieri, E. 2021. Ambystoma maculatum (Spotted Salamander). Aberrant coloration. Herpetological Review 52: 594–595.
- Blais, B.R. and T.A. Sprague. 2020. Ambystoma mavortium mavortium (Barred Tiger Salamander). Aberrant coloration. Herpetological Review 51: 805–806.
- Bogart, J.P., J.E. Linton, and A. Sandilands. 2017. A population in limbo: Unisexual salamanders (genus *Ambystoma*) decline without sperm-donating species. *Herpetological Conservation and Biology* 12: 41–55.
- Bonnet, X., R. Shine, and O. Lourdais. 2002. Taxonomic chauvinism. Trends in Ecology and Evolution 17: 1–3. https://doi.org/10.1016/S0169-5347(01)02381-3.
- Bordzilovskaya, N.P. and T.A. Dettlaff. 1979. Table of stages of the normal development of axolotl embryos and the prognostication of timing of successive developmental stages at various temperatures. *Axolotl Newsletter* 7: 2–22.
- Brandt, B.B. 1952. Albino Ambystoma maculatum. Herpetologica 8: 3.
- Britcher, H.W. 1898. An occurrence of albino eggs of the spotted salamander, *Ambystoma punctatum* L. *Transactions of the American Microscopical Society* 20: 69–74. https://doi.org/10.2307/3221249.
- Cahn, A.R. 1930. A set of albino eggs of *Ambystoma microstoum. Copeia* 1930: 18–19. https://doi.org/10.2307/1436309.
- Camp, E. and M. Lardelli. 2001. Tyrosinase gene expression in zebrafish embryos. Development Genes & Evolution 211: 150–153. https://doi.org/10.1007/ s004270000125.
- Campbell, J.R. 2011. *Ambystoma opcaum* (Marbled Salamander). Albinism. *Herpetological Review* 42: 80–81.
- Childs, H.E., Jr. 1953. Selection by predation on albino and normal spadefoot toads. *Evolution* 7: 228–233. https://doi.org/10.1111/j.1558-5646.1953. tb00084.x.
- Childs, H.E., Jr. and W.E. Howard. 1955. *The Vertebrate Fauna of the San Joaquin Experimental Range*. California Forest and Range Experiment Station, Berkeley, California, USA.
- Collins, J.T. 1965. A population study of *Ambystoma jeffersonianum*. Journal of the Ohio Herpetological Society 5: 61.
- Cortés-Vázquez, S., D. Cruz-Sáenz, and L.D. Wilson. 2016. Notes on a leucistic Ambystoma flavipiperatum Dixon, 1963 (Caudata: Ambystomatidae). Mesoamerican Herpetology 3: 1077–1080.
- Deegan, B., J. Berkholtz, and H. Golet. 1998. Ambystoma opcaum (Marbled Salmander) Albinism. Herpetological Review 29: 229.
- Duellman, W.E. and L.T. Trueb. 1994. *Biology of Amphibians*. The Johns Hopkins University Press, Baltimore, Maryland, USA.
- Dumont, J.N. and J.J. Eppig, Jr. 1971. A method for the production of pigmentless eggs in *Xenopus laevis. Journal of Experimental Zoology* 178: 307–311. https:// doi.org/10.1002/jez.1401780304.
- Dyrkacz, S. 1981. *Recent Instances of Albinism in North American Amphibians and Reptiles.* The Society for the Study of Amphibians and Reptiles, Athens, Ohio, USA.
- Easterla, D.A. 1968. Melanistic spotted salamanders in northeast Arkansas. *Herpetologica* 24: 330–331.
- Etard, A., S. Morrill, and T. Newbold. 2020. Global gaps in trait data for terrestrial vertebrates. *Global Ecology and Biogeography* 29: 2143–2158. https://doi. org/10.1111/geb.13184.

- Frost, S.K. and G.M. Malacinski. 1980. The developmental genetics of pigment mutants in the Mexican axolotl. *Developmental Genetics* 1: 271–294.
- Frost-Mason, S.K. and K.A. Mason. 1996. What insights into vertebrate pigmentation has the Axolotl model system provided? *International Journal of Developmental Biology* 40: 685–693.
- Garcia, T.S., R. Straus, and A. Sih. 2003. Temperature and ontogenetic effects on color change in the larval salamander species *Ambystoma barbouri* and *Ambystoma texanum. Canadian Journal of Zoology* 81: 710–715. https://doi. org/10.1139/z03-036.
- Hall, J.M. 2020. Ambystoma opacum (Marbled Salamander) Coloration. Tennessee Journal of Herpetology 3: 37.
- Harris, S.H. 1967. Albinism in the Jefferson salamander, *Ambystoma jeffersonianum* Green. *Bulletin of the Maryland Herpetological Society* 3: 99–100.
- Harsa-King, M.L. 1980. Melanogenesis in oocytes of wild-type and mutant albino axolotls. *Developmental Biology* 74: 251–262. https://doi.org/10.1016/0012-1606(80)90428-5.
- Hartzell, S.M. 2020. An amelanistic spotted salamander, Ambystoma maculatum (Caudata: Ambystomidae) from eastern Pennsylvania. Herpetology Notes 13: 179–180.
- Hegna, R.H., R.A. Saporito, and M.A. Donnelly. 2013. Not all colors are equal: predation and color polytypism in the aposematic poision frog *Oophaga pumilio. Evolutionary Ecology* 27: 831–845. https://doi.org/10.1007/s10682-012-9605-z.
- Henle, K., A. Dubois, and V. Vershinin. 2017a. Commentated glossary, terminology and synonymies of anomalies in natural populations of amphibians. *Mertensiella* 25: 9–48.
- Henle, K., A. Dubois, and V. Vershinin. 2017b. A review of anomalies in natural populations of amphibians and their potential causes. *Mertensiella* 25: 57–164.
- Hensley, M. 1959. *Albinism in North American Amphibians and Reptiles*. Michigan State University Museum, Lansing, Michigan, USA.
- Houillon, C. and J.T. Bagnara. 1996. Insights into pigmentary phenomena provided by grafting and chimera formation in the axolotl. *Pigment Cell Research* 9: 281–288. https://doi.org/10.1111/j.1600-0749.1996.tb00119.x.
- Humphrey, R.R. 1967. Albino axolotls from an albino tiger salamander through hybridization. *The Journal of Heredity* 58: 95–101. https://doi.org/10.1093/ oxfordjournals.jhered.a107572.
- Jablonski, D., A. Alena, P. Vlček, and D. Jandzik. 2014. Axanthism in amphibians: A review and the first record in the widespread toad of the *Bufotes viridis* complex (Anura: Bufonidae). *Belgian Journal of Zoology* 144: 93–101. https:// doi.org/10.26496/bjz.2014.69.
- Jones, R.G. 1991. Ambystoma texanum (Smallmouth Salamander). Albinism. Herpetological Review 22: 128–129.
- Kaczmarski, M. 2018. Albino clutch of moor frog *Rana arvalis* a rare observation from Poland. Fragmenta Faunistica 61: 61–64. https://doi.org/10.3161/001 59301FF2018.61.1.061.
- Krecsák, L. 2008. Albinism and leucism among European viperinae: A review. *Russian Journal of Herpetology* 15: 97–102. https://doi.org/10.30906/1026-2296-2019-15-%S-97-102.
- Kamaraj, B. and R. Purohit. 2014. Mutational analysis of oculocutaneous albinism: a compact review. *BioMed Research International* 2014: 905472-10. http:// dx.doi.org/10.1155/2014/905472.
- Licht, L.E. and K.P. Grant. 1997. The effects of ultraviolet radiation on the biology of amphibians. *American Zoologist* 37: 137–145. https://doi.org/10.1093/ icb/37.2.137.
- Lowcock, L.A. 1985. An albinistic yellow-spotted salamander, Ambystoma maculatum, from Oak Bay, Quebec. The Canadian Field-Naturalist 99: 105–106.
- McCardle, H. 2012. Albinism in wild vertebrates. Unpublished M.S. thesis, Texas State University-San Marcos, San Marcos, Texas, USA.
- Mitchell, J.C. and D.R. Church. 2002. Leucistic Marbled Salamanders (Ambystoma opacum) in Virginia. Banisteria 20: 67–69.
- Montoliu, L., K. Grønskov, A.H. Wei, M. Martínez-García, A. Fernández, B. Arveiler, F. Morice-Picard, S. Riazuddin, T. Suzuki, Z.M. Ahmed, T. Rosenberg, and W. Li. 2014. Increasing the complexity: new genes and new types of albinism. Pigment Cell & Melanoma Research 27: 11–18. https:// doi.org/10.1111/pcmr.12167.
- Nachman, M.W., H.E. Hoekstra, and S.L. D'Agostino. 2003. The genetic basis of adaptive melanism in pocket mice. *Proceedings of the National Academy*

of Sciences of the United States of America 100: 5268-5273. https://doi.org/10.1073/pnas.0431157100.

- Niedzwiecki, J.H. 2005. Evolutionary history and hybridization of two mole salamander sister species from different habitats. Unpublished Ph.D. Dissertation, University of Kentucky, Lexington, Kentucky, USA.
- Niemiller, M.L. and R.G. Reynolds. 2011. *The Amphibians of Tennessee*. The University of Tennessee Press, Knoxville, Tennessee, USA.
- Niemiller, M.L., B.M. Glorioso, C. Nicholas, J. Phillips, J. Rader, E. Reed, K.L. Sykes, J. Todd, G.R. Wyckoff, E.L. Young, and B.T. Miller. 2009. Notes on the reproduction of the Streamside Salamander, *Ambystoma barbouri*, from Rutherford County, Tennessee. *Southeastern Naturalist* 8: 37–44.
- Nishioka, M., H. Ohtani, and M. Sumida 1987. Chromosomes and the sites of five albino gene loci in the *Rana nigromaculata* group. *Scientific Report of the Laboratory for Amphibian Biology, Hiroshima University* 9: 1–52.
- Nishioka, M. and H. Ueda. 1985. Genetics and morphology of 13 albino stocks in the Rana nigromaculata group. Scientific Report of the Laboratory for Amphibian Biology, Hiroshima University 7: 1–121.
- Olsson, M., D. Stuart-Fox, and C. Ballen. 2013. Genetics and evolution of colour patterns in reptiles. *Seminars in Cell & Developmental Biology* 24: 529–541. https://doi.org/10.1016/j.semcdb.2013.04.001.
- Palis, J.G., A.M. Grosse, and R.E. Dellinger. 2020. Ambystoma mabeei (Mabee's Salamander). Aberrant coloration. Herpetological Review 51: 287–288.
- Petranka, J.W. 1998. *Salamanders of the United States and Canada*. Smithsonian Institution Press, Washington, DC, USA.
- Piatt, J. 1951. Transplantation experiments between pigmentless and pigmented eggs of *Amblystoma punctatum. Journal of Experimental Zoology* 118: 101–135. https://doi.org/10.1002/jez.1401180106.
- Piatt, J. 1966. Origin and development of retinal melanin in *Amblystoma punctatum* devoid of ovarian pigment. *Journal of Experimental Zoology* 163: 247–257. https://doi.org/10.1002/jez.1401630304.
- Protas, M.E., C. Hersey, D. Kochanek, Y. Zhou, H. Wilkens, W.R. Jeffery, L.I. Zon, R. Borowsky, and C.J. Tabin. 2006. Genetic analysis of cavefish reveals molecular convergence in the evolution of albinism. *Nature Genetics* 38: 107– 111. https://doi.org/10.1038/ng1700.
- Protas, M.E. and N.H. Patel. 2008. Evolution of coloration patterns. *The Annual Review of Cell and Developmental Biology* 24: 425–446. https://doi.org/10.1146/annurev.cellbio.24.110707.175302.
- Reiter, M.K., C.D. Anthony, and C.M. Hickerson. 2014. Territorial behavior and ecological divergence in a polymorphic salamander. *Copeia* 2014: 481–488. https://doi.org/10.1643/CE-13-154.
- Riley, S.P.D., H.B. Shaffer, S.R. Voss, and B.M. Fitzpatrick. 2003. Hybridization

between a rare, native Tiger Salamander (*Ambystoma californiense*) and its introduced congener. *Ecological Applications* 13: 1263–1275. https://doi. org/10.1890/02-5023.

- Rivera, X., O. Arribas, and F. Marti. 2001. Anomalías pigmentarias en anfibios y reptiles. *Quercus* 180: 18–22.
- Rye, L.A. 1991. A leucistic eastern redback salamander, *Plethodon cinereus*, and an albinistic yellow-spotted salamander, *Ambystoma maculatum*, from southern Ontario. *The Canadian Field-Naturalist* 105: 573–574.
- Salthe, S.N. 1969. Reproductive modes and the number and sizes of ova in the urodeles. *The American Midland Naturalist* 81: 467–490. https://doi. org/10.2307/2423983.
- Simpson, J.F. and T.P. Wilson. 2010. Ambystoma opacum (Marbled Salamander). Coloration. Herpetological Review 41: 185–186.
- Smith, P.B. and M.C. Michener. 1962. An adult albino Ambystoma. Herpetologica 18: 67–68.
- Soares, D. and M.L. Niemiller. 2020. Extreme adaptation in caves. *The Anatomical Record* 303: 15–23. https://doi.org/10.1002/ar.24044.
- Stephenson, B.P. and K.M. Drace. 2014. A new report of albinism in the Common Garter Snake (*Thamnophis sirtalis*), and a review of existing records: Is there a geographic bias in observations. *Herpetological Review* 45: 569–577.
- Szydłowski, P., J.P. Madej, M. Duda, J.A. Madej, A. Sikorska-Kopyłowicz, A. Chełmońska-Soyta, L. Ilnicka, and P. Duda. 2020. Iridophoroma associated with the lemon frost colour morph of the leopard gecko (*Eublepharis macularius*). *Scientific Reports* 10: 5734. https://doi.org/10.1038/s41598-020-62828-9.
- Thibaudeau, G. and R. Altig. 2012. Coloration of anuran tadpoles (amphibia): development, dynamics, function, and hypotheses. *International Scholarly Research Network Zoology* 2012: 725203. https://doi.org/10.5402/2012/725203.
- Trauth, S.E. and M.E. Cartwright. 1989. An albino larva in the ringed salamander, *Ambystoma annulatum*, from Arkansas. *Bulletin of the Chicago Herpetological Society* 24: 128.
- Underhill, D.K. 1968. Albino eggs and larvae of *Ambystoma texanum* in central Illinois. *Herpetologica* 24: 266.
- Wallace, R.A. and K. Selman. 1990. Ultrastructural aspects of oogenesis and oocyte growth in fish and amphibians. *Journal of Electron Microscopy Technique* 16: 175–201. https://doi.org/10.1002/jemt.1060160302.
- Waltson, L.J. and K.J. Register. 2004. Ambystoma opacum (Marbled Salamander). Frequency of albino life stages. Herpetological Review 35: 365.
- White, J. 2002. Ambystoma maculatum (Spotted Salamander). Castebeiana 22: 17.
- White, J. 2008. Ambystoma maculatum (Spotted Salamander). Color variation. Castebeiana 28: 67–68.