Experimental Support for Aposematic Coloration in the Salamander *Ensatina eschscholtzii xanthoptica*: Implications for Mimicry of Pacific Newts

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A field experiment was conducted to test the hypothesis that the plethodontid salamander *Ensatina eschscholtzii xanthoptica* benefits from aposematic coloration. Under field conditions, clay models painted to resemble *E. e. xanthoptica* were attacked significantly less often than models lacking the supposed aposematic colors. In addition, the head region of models was attacked significantly more frequently than random, suggesting the models were perceived as prey items. These results are consistent with the hypothesis that *E. e. xanthoptica* is a mimic of highly toxic Pacific Newts in the genus *Taricha*. The significance of the *E. e. xanthoptica* phenotype for the ring species biogeographic scenario and future research directions are briefly discussed.

APOSEMATIC, or warning, signals function to advertise noxious or hazardous properties (Poulton, 1890; Cott, 1940). Well-known herpetological examples include the auditory rattle of venomous rattlesnakes (*Crotalus, Sistrurus*; Greene, 1988), the conspicuous colors of toxic poison dart frogs (Dendrobatidae; Summers and Clough, 2001) and the orange ventral coloration of Pacific Newts (*Taricha*; Johnson and Brodie, 1975). In many instances, predators learn from experience to avoid potential prey items displaying warning signals, but in some cases avoidance is innate (Edmunds, 1974; Smith, 1975; Pough, 1988).

Species with aposematic colors are susceptible to mimicry by unrelated species. Two varieties of mimicry are widely recognized: Müllerian mimicry (Müller, 1879) results when noxious species resemble one another, and Batesian mimicry (Bates, 1862) results when palatable species evolve resemblance to noxious or dangerous species. In the former case, both species contribute to and benefit from predator learning (but see Speed, 1993). In the latter, only the noxious species (the model) participates in predator learning; the mimic is parasitic on the model signal, and thereby degrades the effectiveness of that signal for the model. For this reason, Batesian mimicry functions best when the model is encountered by predators more frequently than the mimic (Edmunds, 1974).

The Yellow-Eyed Ensatina, *Ensatina eschscholtzii xanthoptica*, is hypothesized to be a Batesian mimic of highly toxic, aposematic Pacific Newts in the genus *Taricha* (Stebbins, 1949; Wake et al., 1989), with which it co-occurs in the San Francisco Bay region and the foothills of the Sierra Nevada, California. Here I report on experimental results consistent with the hypothesis that *E. e. xanthoptica* benefits from reduced predation because it possesses aposematic coloration similar to that of *Taricha*. The implications of these results for mimicry of *Taricha* by *E. e. xanthoptica* are considered.

Two species of Pacific newt, *T. torosa torosa* (California Newt) and *T. granulosa* (Rough-Skinned Newt), are sympatric with *E. e. xanthoptica* in the San Francisco Bay region, and *T. t. sierrae* (Sierra Newt) is sympatric with *E. e. xanthoptica* in the Sierra Nevada. *Taricha t. torosa*, *T. t. sierrae*, and *T. granulosa* are similarly colored: all have a solid dark brown dorsum, a reddish, orange, or yellow belly, and bold yellow patches in the iris above and below the pupil. Eyelid coloration varies from brown to orange. The bright ventral coloration is exposed to potential predators via an unken reflex, a posture in which the back is strongly arched, lifting the head and tail over the body and depressing the belly against the substrate; in addition, the eyes are closed and depressed, and the limbs are extended stiffly outward (Riemer, 1958; Brodie, 1977). The unken reflex, in conjunction with the orange ventral coloration, has been shown experimentally to function as an aposematic signal (Johnson and Brodie, 1975).

The *E. e. xanthoptica* phenotype is similar to *Taricha*, including a solid brown dorsum, a solid orange belly coloration (which commonly extends further onto the side of the body than seen in *Taricha*), dense yellow iridic eye patches, and brown-orange to orange eyelids. Additionally, *E. e. xanthoptica* has a solid band of orange coloration across the dorsal surface of its proximal limb segments, and a patchy orange network on the dorsal surface of its distal limb seg-

ments. Note that the paintings of *E. e. xanthoptica* in Stebbins (2003; Plate 7) are understated in their depiction of the orange coloration (but see the photo, p. 176). Harassed *E. e. xanthoptica* stand on their toes stiff-legged, arch their back down, hold the neck erect with the head horizontal or downward, and lash their tails at attackers (Stebbins, 1951; Brodie, 1977). This behavior differs from the unken reflex of *Taricha* in that the tail and head are not raised directly above the body, but it does effectively display the orange coloration on the side and ventral portions of the body. It also draws attention to the tail, where the toxins are concentrated (Brodie, 1983). *Taricha* and *E. e. xanthoptica* are similar in size, though *Taricha* is more robust.

All species of *Taricha* possess the neurotoxin tetrodotoxin (TTX), especially in the skin (Twitty and Johnson, 1934; Wakely et al., 1966; Hanifin, 1999). There exists strong geographic variation in TTX levels throughout the range of *Taricha* (Hanifin et al., 1999), but individuals in the San Francisco Bay region are known to be highly toxic. For example, Brodie et al. (1974) showed that individuals of *T. torosa* from near Orinda, Contra Costa County (~5 km from the location of the experiment reported on herein) possess sufficient TTX to kill 1,200–2,500 20 g mice. This extreme level of toxicity is hypothesized to be the result of a coevolutionary arms race between *Taricha* toxicity and resistance by the common garter snake, *Thamnophis sirtalis* (Brodie and Brodie, 1990, 1991; Brodie et al., 2002). Recent work has shown the San Francisco Bay region and the foothills of the Sierra Nevada (both regions where *E. e. xanthoptica* and *Taricha* co-occur) to be "hotspots" of *Thamnophis* resistance to TTX, and thus likely hotspots of *Taricha* toxicity (see Brodie et al., 2002: Fig. 5).

Predation is difficult to observe in natural populations, especially on small, secretive animals. Documented predators of *E. eschscholtzii* include Steller's Jays (*Cyanocitta stelleri*; Stebbins, 1954), garter snakes (*Thamnophis* sp.; Beneski, 1989; Fitch, 1940), and raccoons (*Procyon lotor*; Wake et al., 1989). Stebbins (1954) discusses other possible predators. The only known major predator of adult *Taricha* is *Thamnophis sirtalis*. Avian predators occasionally eat *Taricha* with fatal consequences (reviewed in Mobley and Stidham, 2000). To test the hypothesis that *E. e. xanthoptica* benefits from its orange and yellow coloration, field predation experiments employing painted clay models were conducted. Similar experiments have proven useful in detecting predation on color patterns in the field with natural predators in other systems (e.g., Brodie,

1993; Schneider et al., 1999; Pfennig et al., 2001).

MATERIALS AND METHODS

Model construction.—Models were made by pouring melted, non-toxic, grey VanAken Modeling Clay into a mold made from a formalin-fixed *E. eschscholtzii* carcass. Models were 120 mm total length and 62 mm snout-vent length. In addition, two 5 mm diameter plastic half spheres were imbedded into the clay on either side of the head to create protuberant eyes. Models were painted to produce two morphs. The first, similar to *E. e. xanthoptica* ("orange" morph), had a brown dorsum, a yellow patch above the iris in an otherwise black eye, and an orange venter, eyelids, and proximal limb segments; the distal limb segments and feet were given a brown base color lightly mottled with orange flecks. This model is as vivid as the most brightly colored *E. e. xanthoptica*. The second morph had a brown dorsal surface, legs, toes, and eyelid, a flesh-colored ventral surface (similar to the subspecies *E. e. eschscholtzii* and *E. e. oregonensis*), and a solid black eye. This model thus lacks the hypothesized aposematic colors of the orange morph, and is called the "brown" morph. Dorsal and ventral colors were applied with Painters Touch spray paint; additional colors on the eyes and limb segments were hand painted with Americana Acrylic Paints. A final enamel gloss (Rust-Oleum) was added to all models to give the shiny, wet look of an amphibian. The advantage of using clay for predation experiments is that soft clay retains predatory marks (Brodie, 1993); in this experiment, a hard outer layer of paint had to be penetrated for a mark to be clearly recorded, unlike experiments employing colored plasticine, and, as a result, determining the class of predator was sometimes difficult.

Transect placement.—Models were placed in closed canopy woodland on East Bay Municipal Unity District land, Contra Costa County, California, near Wildcat Canyon and San Pablo Dam roads. This property is protected from public access, and is regularly patrolled. The dominant trees are California bay (*Umbellularia californica*) and coast live oak (*Quercus agrifolia*). The dominant understory shrub is poison oak (*Toxicodendron diversilobum*). Western Scrub Jays (*Aphelocoma californica*), Steller's Jays (*Cyanocitta stelleri*), American Crows (*Corvus brachyrhynchos*), and raccoons (*Procyon lotor*) are common on the property (pers. obs). Four hundred and fifty-four models were placed along nine transects. Transects were hundreds of meters to kilome-

ters apart, with open grassland separating them. Each transect had 25 models of each morph (50 models per transect). The exceptions are two transects with 53 models (27 brown, 26 orange) and 51 models (26 brown, 25 orange). Models were located at 10 m intervals, and spaced such that every ten models on each transect contained five orange and five brown morphs in random order. This design prevented severe clumping of morphs, yet maintained the haphazard arrangement. To eliminate crypsis as a confounding factor, all models were glued (with Elmer's glue) to a 8.5×5.5 inch piece of dull white "Rite in the Rain" paper, which was stapled to a 1 ft^2 piece of aged (three years outside), 1/8 inch plywood base. Transects were placed to track the oak woodland habitat, and avoided unsuitable habitat such as large clearings. On this property, oak woodland typically adjoins seasonal streams, with grassland between patches of woodland. *Taricha torosa* and *E. e. xanthoptica* are abundant, and *T. granulosa* is less common but present (pers. obs). Models were placed on 4–6 March and collected on 27–29 March 2001 (24 to 25 days per transect) for a total of 11,123 model days.

Scoring Predation Attempts and Statistical Testing.— Marks on models were scored as attacks, and the location was categorized as head, torso, limbs, and tail. The hard outer layer of paint often made predator identification impossible, so attacks were not sorted by predator. If some categories of predators (e.g., birds) discriminate among model morphs but others (e.g., small rodents) do not, then combining attacks will result in conservative statistical tests.

To compare the frequency of attacks among model morphs, models were scored as either attacked or not (multiple attack marks on the same model were counted as a single attack). To determine whether attacks were non-randomly directed at particular body regions (head, torso, limbs, and tail), the proportion of attacks to body regions was compared with the relative volumes of those regions. G-tests were used to assess statistical significance (Sokal and Rohlf, 1995), with $P \leq 0.05$ accepted as significant.

RESULTS

Models were visually scored for attack marks. In some cases, it was possible to identify the predator (e.g., mammalian incisor marks, bird peck marks; Fig. 1A, C), but precise determination was often difficult (Fig. 1B, D). A total of 71 models (15.6%) were attacked. Most attacked models had one to three attack marks, 16 showed signs of attack to more than one body part, seven models were virtually destroyed, and three were missing (missing models were included in the analyses, but the results are the same when missing models are excluded from the analyses).

There was no significant heterogeneity in attack rate on the color morphs among transects ($G_H = 7.559$, df = 8, ns). When data from transects are combined, the brown morphs were attacked nearly twice as often as orange morphs (46 to 25: $G = 7.35$, df = 1, $P = 0.007$). To eliminate the possibility that a small number of individual predators were responsible for this result, models attacked in spatial clusters (i.e., two or more adjacent attacked models) were removed from the dataset and the analysis repeated, with the same qualitative results (37 Brown vs. 4 Orange, $G = 11.783$, df = 1, $P = 0.0006$).

The distribution of attacks on body regions was non-random relative to the volume of those body regions. When all the attacked models are combined, the head was attacked significantly more frequently (33% of attacks) than its volumetric proportion (17%) ($G = 6.921$, df = 1, $P = 0.01$) (Fig. 2); conversely, the torso was attacked significantly less frequently (15%) than its volumetric proportion (40%) ($G = 16.123$, df = 3, $P < 0.001$) (Fig. 2). The same results are found for each morph separately, with the head attacked more often, and the torso less often, than predicted given their volumetric proportions ($P < 0.05$).

DISCUSSION

The orange morph was attacked significantly fewer times than the brown morph. This result is consistent with the hypothesis that the *E. e. xanthoptica* phenotype reduces predation rates by virtue of its orange and yellow coloration, which noticeably resembles *Taricha*. The placement of all models on a white background served as a control for crypsis; all models were conspicuous. Because the models were placed in nine spatially separated transects, and because results are more robust when models attacked in spatial clusters are removed from the analysis, the possibility of attack by one or a few predators is unlikely.

The non-random distribution of attacks suggests that the models were perceived by predators as prey. The volume of the head was 15% of the model volume, but 33% of all attacks were directed at the head. Some predators are known to direct attacks at the heads of prey
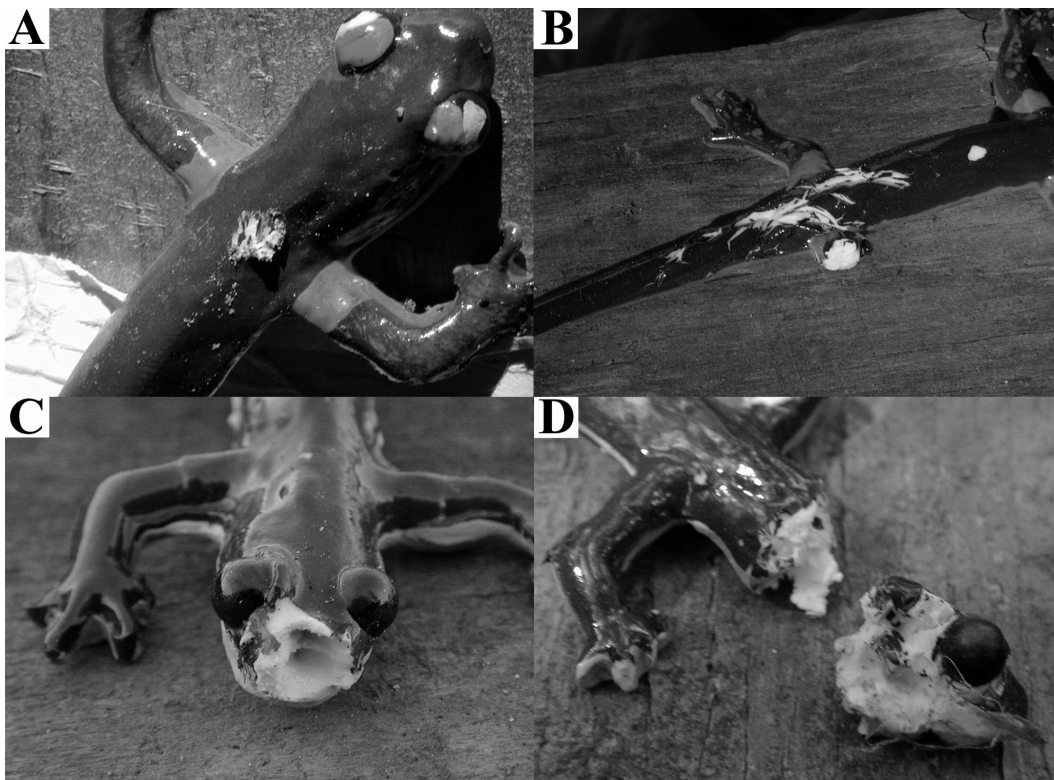
Fig. 1. Representative attacked plasticine models. (A) Avian peck mark on an orange morph. (B) Heavily damaged orange morph, predator unknown. (C) Rodent incisor marks on the snout of a brown morph. (D) Heavily damaged head region of a brown morph, predator unknown.
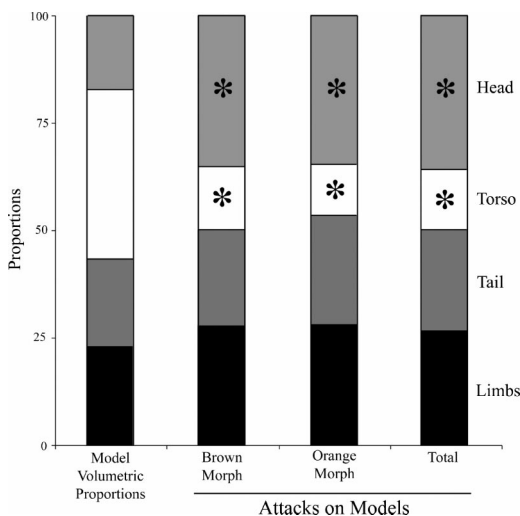

Fig. 2. Comparison of the proportion of attacked body regions (head, torso, tail, and limbs) relative to the volumetric proportions of those regions. * indicates the proportion of attacks differs significantly from the proportion expected if attacks were random relative to volume ($P < 0.05$).

items, especially dangerous and noxious prey. For instance, Loggerhead Shrikes (*Lanius ludovicianus*) and Motmots (*Eumomota superciliosa*) preferentially attack the head region of models (Smith, 1973, 1976). Brandon and Huheey (1975) report two field observations in which the head region of *Plethodon jordani* (a terrestrial, nocturnal, mildly noxious salamander) was targeted in predation attempts by American Robins (*Turdus migratorius*). In addition, Brandon et al. (1979) report that chickens (White Leghorn Cockerels) repeatedly pecked anesthetized *Pseudotriton montanus diasticus* (also a terrestrial, nocturnal, and mildly noxious salamander) ''usually on the head'' (p. 296).

It is not yet clear whether *E. e. xanthoptica* is itself aposematic (and potentially a Müllerian mimic of *Taricha*), or a palatable Batesian mimic of *Taricha. Ensatina eschscholtzii* is known to possess poison glands, particularly in the tail, that produce a sticky, milky secretion and function to deter predation (Hubbard, 1903; Stebbins, 1954; Beneski, 1989). *Ensatina* can autotomize their tails at the base, and autotomized tails bend wildly for several minutes (Stebbins, 1954;

Wake and Dresner, 1967). However, aside from *E. e. xanthoptica*, all morphs of *E. eschscholtzii* are considered cryptic (Stebbins, 1949; Brown, 1974; Wake et al., 1989), suggesting that *E. eschscholtzii* is not sufficiently toxic to benefit from aposematic coloration. No data exist on geographic variation in toxicity; however, it is conceivable that *E. e. xanthoptica* is less palatable than other morphs. It would be useful to show that individuals of *E. eschscholtzii* (including *E. e. xanthoptica*) are sufficiently palatable to serve as a food item when consumed by visual predators. To distinguish among the aposematic coloration and Batesian mimicry hypotheses, one must demonstrate that known visual predators (such as corvids) are "tricked" into avoiding *E. e. xanthoptica* following a negative experience with *Taricha*. Experiments are currently being planned to examine the interactions between *E. eschscholtzii*, *Taricha*, and potential avian predators.

Examples of mimicry of newts by terrestrial plethodontid salamanders are known. In the eastern United States, the red eft stage of the toxic Red-Spotted Newt, *Notophthalmus viridescens*, is thought to be mimicked by an erythristic morph of *Plethodon cinerius* (Brodie and Brodie, 1980; Tilley et al., 1982), by *Pseudotriton ruber* (e.g., Howard and Brodie, 1971; Huheey and Brandon, 1974; Pough, 1974), and perhaps by *Gyrinophilus porphyriticus* (Howard and Brodie, 1973; Brandon et al., 1979). Newts are ideal organisms for the evolution of a mimicry system because of their extreme toxicity (Brodie, 1968; Brodie et al., 1974; Hanifin et al., 1999), and their conspicuous diurnal activity. Visually oriented predators have ample opportunity to experience newts, and either learn or evolve avoidance behaviors. All the proposed mimics of newts are nocturnal, mildly noxious, and not identical in appearance to their model. Diurnal avian predators are certainly known to locate and prey upon nocturnal salamanders (e.g., Brandon and Huheey, 1975; Rubinoff, 1996; Reaser, 1997), but they probably do not encounter them with regularity. In such systems, imperfect mimicry can be effective when the model is sufficiently dangerous (Caley and Schluter, 2002).

There are seven subspecies in the *Ensatina* complex, each differentiated in coloration and color pattern (Stebbins, 1949). With the exception of *E. e. xanthoptica*, all subspecies are hypothesized to be cryptic (Stebbins, 1949; Brown, 1974; Wake et al., 1989), either via background matching (the subspecies *E. e. picta*, *E. e. oregonensis*, *E. e. eschscholtzii*) or disruptive coloration (*sensu* Cott, 1940) (*E. e. platensis*, *E. e. croceater*, *E. e. klauberi*). However, this manuscript reports on the first empirical evidence of the ecological function of a phenotype in the *Ensatina* complex. Research on the ecological function of the diverse color patterns in the *Ensatina* complex is key to understanding diversification. This is because *E. eschscholtzii* is considered an example of a "ring species" (Wake and Yanev, 1986; Moritz et al., 1992; Irwin et al., 2001), and adaptive diversification is an important component of the ring species biogeographic scenario (Stebbins, 1949; Brown, 1974; Wake et al., 1989). The subspecies *E. e. xanthoptica* is of particular importance because of its central geographic position. In the San Francisco Bay region, *E. e. xanthoptica* forms multiple secondary contact zones with *E. e. oregonensis* and *E. e. eschscholtzii* (Wake, 1997), and in the foothills of the Sierra Nevada (which were colonized by San Francisco Bay populations; Wake et al., 1989; Wake and Yanev, 1986; Moritz et al., 1992) there is a spatially extended secondary contact between *E. e. xanthoptica* and *E. e. platensis* (Wake et al., 1989; Alexandrino et al., in press). There is an ongoing debate regarding the taxonomy of the *Ensatina* complex, with some authors advocating the recognition of multiple species (Frost and Hillis, 1990; Highton, 1998, 2000), and others defending the current taxonomy of a single polytypic species (Moritz et al., 1992; Wake and Schneider, 1998; Wake and Jockusch, 2000). Data on the interactions of lineages where they contact will be vital to resolution of the dispute, and studies of the ecological function of the divergent phenotypes in *Ensatina* will contribute to understanding those interactions.

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