

WHY DOES THE YELLOW-EYED ENSATINA HAVE YELLOW EYES? BATESIAN MIMICRY OF PACIFIC NEWTS (GENUS *TARICHA*) BY THE SALAMANDER *ENSATINA ESCHSCHOLTZII XANTHOPTICA*

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Color patterns commonly vary geographically within species, but it is rare that such variation corresponds with divergent antipredator strategies. The polymorphic salamander *Ensatina eschscholtzii*, however, may represent such a case. In this species, most subspecies are cryptically colored, whereas *E. e. xanthoptica*, the Yellow eyed ensatina, is hypothesized to be an aposematic mimic of highly toxic Pacific newts (genus *Taricha*). To test the mimicry hypothesis, we conducted feeding trials using Western Scrub-Jays, *Aphelocoma californica*. In every feeding trial, we found that jays, following presentation with the presumed model (*T. torosa*), were more hesitant to contact the presumed mimic (*E. e. xanthoptica*) than a control subspecies lacking the postulated aposematic colors (*E. e. oregonensis*). The median time to contact was 315 sec for the mimic and 52 sec for the control. These results support the mimicry hypothesis, and we suggest that *E. e. xanthoptica* is likely a Batesian mimic, rather a Müllerian or quasi-Batesian mimic, of Pacific newts.

KEY WORDS: Batesian mimicry, *Ensatina eschscholtzii*, Müllerian mimicry, predation, quasi-Batesian mimicry, ring species, *Taricha*, Western Scrub-Jay.

The risk of predation is pervasive in nature, and prey species have evolved a variety of defenses that reduce the likelihood of attack by predators, such as various mechanisms of crypsis, or by rendering

themselves unprofitable to predators (Ruxton et al. 2004). Organisms with noxious or deadly defenses commonly possess conspicuous warning signals, or aposematism (Poulton 1890; Cott 1940), which advertises their unprofitability and enhances predator learning (e.g., Roper and Redston 1987). Not all aposematic signals are honest, however, because in many instances edible species copy the aposematic signals of defended species. This phenomenon, called Batesian mimicry (Bates 1862), contrasts with Müllerian mimicry (Müller 1879), whereby defended species evolve to share

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a common aposematic signal due to selection for shared predator learning.

Although one might expect purifying selection to maintain a single warning signal, which may promote predator learning, aposematic coloration often exhibits complex patterns of differentiation across the range of species (Mallet and Joron 1999). Tremendous color pattern variation is found within the aposematically colored Strawberry poison frog, *Dendrobates pumilio*, for instance (Siddiqi et al. 2004). Seldom, however, does geographic variation in color pattern include divergent antipredator strategies, such as various mechanisms of crypsis and aposematic coloration. Such a situation may be found in the polymorphic salamander ring species *Ensatina eschscholtzii*. In *E. eschscholtzii*, seven subspecies are recognized, six of which are thought to be either cryptic by way of background matching (*E. e. oregonensis*, *E. e. picta*, and perhaps *E. e. eschscholtzii*) or disruptive coloration (*E. e. platensis*, *E. e. croceater*, *E. e. klauberi*) (Stebbins 1949). In contrast, *E. e. xanthoptica*, the Yellow-eyed salamander, is hypothesized to be a mimic of highly toxic, aposematically colored newts in the genus *Taricha* (Stebbins 1949; Brown 1974; Kuchta 2005). Two species of newt, *T. granulosa* (Rough-skinned newt) and *T. torosa* (California newt), overlap the range of *E. e. xanthoptica*. All three species possess a similar phenotype, including a brown

back, a striking orange ventral region, and bold yellow patches in the iris; some individuals have orange upper eyelids as well (Fig. 1). *Ensatina eschscholtzii xanthoptica* also possesses orange proximal limb segments, which are brown in *Taricha*. The overall similarity between *Taricha* and *E. e. xanthoptica* led Stebbins (1949) to hypothesize a mimetic relationship between them. Most populations of *Taricha* studied, including those within the range of *E. e. xanthoptica*, possess the potent neurotoxin tetrodotoxin (TTX) in their skin in sufficient quantities to deter or kill most predators, and some populations of *Taricha* are among the most toxic organisms ever found (Brodie et al. 2005 and references therein).

To test the hypothesis that *E. e. xanthoptica* benefits from reduced predation as a consequence of its supposed aposematic (orange and yellow) colors, Kuchta (2005) deployed clay salamander replicas in the field and recorded attack rates. He found that models possessing the yellow and orange colors were depredated significantly less often than models lacking the supposed aposematic colors, suggesting that *E. e. xanthoptica* benefits from aposematic coloration. The study, however, did not directly demonstrate that *E. e. xanthoptica* is an effective mimic of *Taricha*. In addition, *E. e. xanthoptica* possesses granular glands in its skin, with a particularly dense packaging of them in the tail, and therefore, if



Figure 1. Photos of (A) the presumed mimic, *Ensatina eschscholtzii xanthoptica*; (B) the presumed model, *Taricha torosa*; (C) the presumed mimic (*E. e. xanthoptica*; left), and model (*T. torosa*; right) together; and (D) the experimental control, *E. e. oregonensis*, which lacks the aposematic colors and is considered cryptic (Stebbins 1949). Photos A–C were taken by Bill Leonard and are used with permission; photo D by S. R. Kuchta.

E. e. xanthoptica is a mimic of *Taricha*, it is unclear whether that relationship is Batesian or Müllerian.

To test the hypothesis that *E. e. xanthoptica* benefits from a mimetic relationship with *Taricha*, we conducted controlled feeding experiments using live Western Scrub-Jays (Corvidae: *Aphe-locoma californica*) as predators. This species forages diurnally for a wide range of prey items, including small terrestrial vertebrates, and is common throughout the range of *E. e. xanthoptica* (Curry et al. 2002). In our experiment, jays were first presented with a presumed model (*T. torosa*), then they were presented with the presumed mimic (*E. e. xanthoptica*) and a control (*E. e. oregonensis*) in a random order, and the time to first contact measured. The subspecies *E. e. oregonensis* is an ideal control in this experiment because it is identical to *E. e. xanthoptica* in shape and proportions, but lacks the aposematic colors found on *E. e. xanthoptica*.

Methods

EXPERIMENTAL PROTOCOL

Ten Western Scrub-Jays were used as the model predator in the experiment. After a jay was captured, it was immediately banded and released into the aviary in which the feeding trials were conducted. Captured jays were given a two-day acclimation period before the start of the trials. Food (mixed bird seed, dog food, and peanuts) and water were provided ad libitum prior to testing, but the food dish was removed from the cage the evening before all feeding trials. Feeding trials began between 0700 and 1000 h, and only one trial was performed every day on each jay. After the trial, normal food was returned to the cage within 1–4 h; food was not returned immediately so the jays would not associate feeding trials with the return of their food dish.

Salamanders were first euthanized in a carbon-dioxide chamber prior to the start of the feeding trials. Euthanization eliminated behavior and forced the jays to make their decisions based on color and shape alone. Salamanders were presented in a small dish, where they were positioned on top of moist, white paper towels in a life-like posture. All trials were observed from a hidden vantage point. For the first feeding trial, a Slender salamander (*Batrachoseps attenuatus* or *B. luciae*) was presented to the jay for 20 min. The purpose of the *Batrachoseps*, which is edible (Hubbard 2003), was to assure the jay was willing to sample a salamander. If the *Batrachoseps* was not eaten within 20 min, it was removed and the trial was repeated the next day. The day after a jay ate a *Batrachoseps*, it was presented with a *T. torosa* for 20 min to provide a standardized prior exposure with a postulated model species. The following day, jays were given either an *E. e. xanthoptica* (presumed mimic) or an *E. e. oregonensis* (control). The choice was random, but the experiment was constrained to provide an equal number of trials with both subspecies were pre-

sented first. On the final day of the experiment, jays were given the other subspecies of *Ensatina* (i.e., if a jay was first presented with an *E. e. oregonensis*, it was given an *E. e. xanthoptica* the next day, and vice versa). We were interested in determining if Western Scrub-Jays are more hesitant to contact *E. e. xanthoptica* than *E. e. oregonensis* after exposure to *T. torosa*. Our measure was the time to first contact by the jay with the salamander species, because this is likely to be an ecologically relevant measure of predation risk. The *T. torosa*, *E. e. xanthoptica*, and *E. e. oregonensis* used in the feeding trials did not differ significantly in mean snout-to-vent length (ANOVA, $F_{3,39} = 9.4$; Tukey's HSD, $P > 0.05$) or mass (ANOVA, $F_{3,39} = 16.43$; Tukey's HSD, $P > 0.05$), which required that relatively small *T. torosa* and relatively robust *E. e. xanthoptica* and *E. e. oregonensis* were used in the feeding trials; in contrast, the slender salamanders (*B. attenuatus* and *B. luciae*) were significantly shorter and weighed less than the other salamanders (Tukey's HSD, $P < 0.05$). Jays were released immediately following the last feeding trial.

STATISTICAL ANALYSES

Feeding trials were terminated after 20 min, and our data are therefore right censored for subjects that were not contacted. Survival curves were thus used to compare the times to first contact. With survival curves, the parameter of interest, the survival function $S(t)$, is the observed probability of an individual in the population surviving beyond time t . Survival curves were calculated in the statistical program JMP 5.1 (StatSoft, Inc.), and a log-rank test was used to determine if the curves for *E. e. xanthoptica* (the presumed mimic) and *E. e. oregonensis* (the control) differed.

SAMPLING

Experiments were conducted at two localities, starting at the Pepperwood Preserve in Sonoma County (38° 34' 03" N, 122° 41' 18" W). This reserve is northeast of the range of *E. e. xanthoptica* (*E. e. oregonensis* is found there). Western Scrub-Jays were trapped in Potter traps, and immediately transferred to cages constructed of chicken wire (cages approximately 1.2 m wide, 1.5 m tall, and 3.0 m long). All avian subjects fledged at least 6 months prior to testing. Jays were prevented from observing one another by fixing plastic tarps to the walls separating the cages. The first jay was caught on 13 March 2005, and experiments were concluded on 4 April 2005. Three jays were captured and tested during this period. Due to difficulties capturing Western Scrub-Jays at Pepperwood, the experiments were relocated to Hastings Natural History Reservation in Monterey County (36° 23' 07" N, 121° 33' 02" W). This reserve is south of the range of *E. e. xanthoptica* (*E. e. eschscholtzii* is found there). Experiments were conducted at two separate time periods at Hastings. Between 6 December and 13 December 2005, three jays were trapped and tested; and between 12 April and 25 April 2006, five jays were

trapped and tested. Because the two reserves are outside the range of *E. e. xanthoptica*, the jays used in the experiments are unlikely to have had prior experience with the presumed mimic. However, newts are abundant at both study sites (*T. torosa*, *T. granulosa*, and *T. rivularis* at Pepperwood, and *T. torosa* at Hastings), and avian predators likely have had encounters with the presumed model.

Batrachoseps attenuatus was used in feeding trials at the Pepperwood Preserve, and *B. luciae* was used at the Hastings Reservation. These are the local species at the respective reserves, and are cryptic species; very detailed observations are required to distinguish them (Jockusch et al. 2001). Both species are elongate and slender, with reduced limbs and a dorsal stripe that varies from reddish to yellow. The model species, *T. torosa*, was collected directly from the study site (Pepperwood or Hastings). These populations are weakly genetically diverged from one another because populations north of Monterey only recently expanded to their current distribution (Kuchta and Tan 2006). The *E. e. xanthoptica* used in the feeding trials were collected from Strawberry Canyon, Contra Costa County, and the *E. o. oregonensis* were collected along Gazos Creek Road, San Mateo County. Both collection sites are located intermediate to the Pepperwood and Hastings reserves. *Ensatina eschscholtzii xanthoptica* from Strawberry Canyon are brightly colored, whereas the *E. e. oregonensis* from Gazos Creek are bland in coloration, even relative to other *E. e. oregonensis* (S. R. Kuchta, pers. obs.) (Fig. 1).

Results

Of the 11 birds captured, five ate the *Batrachoseps* (Slender salamander) during the first presentation, two ate it on the second day, and three ate it on the third day. One jay refused to eat a *Batrachoseps* and was released without further testing. When presented with the postulated model, *T. torosa*, the jay did not contact the newt in 7 of 10 trials (Fig. 2A). In two trials, the jay poked the *T. torosa* briefly, quickly flipping it out of the presentation dish, but never touched the newt again (Jays G and J). Jay I contacted the newt 30 sec after it was presented, and pecked at it repeatedly for 3 min, but did not attempt to eat the newt or take it into its beak. The postulated mimetic species, *E. e. xanthoptica*, was not touched in 3 of 10 trials, but was eaten in five of the seven trials in which it was touched. The median time to first contact was 315 sec. The control species, *E. e. oregonensis*, was eaten in 9 of 10 feeding trials, and the median time to first contact was 52 sec.

All 10 jays contacted the *E. e. oregonensis* more quickly than the *E. e. xanthoptica* (Fig. 2A). The probability of such a result due to random chance is $0.5^{10} = 0.00098$. The same pattern was also recovered in the survival curves, with the probability of survival at all times higher for *E. e. xanthoptica* than *E. e. oregonensis* (Fig.

2B). The two survival curves are significantly different ($\chi^2 = 4.5042$; $P = 0.0299$).

Discussion

Mimicry systems, although widespread among terrestrial insects such as butterflies (Mallet and Joron 1999; Langham 2004), are not common among vertebrate species (but see Brodie and Brodie 1980; Dumbacher and Fleischer 2001; Symula et al. 2001). Using predation experiments with captive Western Scrub-Jays, we tested the hypothesis that one of the subspecies of the polymorphic ring species *E. e. xanthoptica* is a mimic of highly toxic newts in the genus *Taricha*. When presented with a postulated model species, *T. torosa* (California newt), jays usually did not contact that newt, and never attempted to eat one. Newts are extremely abundant at both study sites (e.g., Trenham 1998; S. R. Kuchta, pers. obs), and it is highly probable that the jays in this study had prior opportunities to be educated on the chemical defenses of newts. Innate avoidance of the newt color pattern cannot be excluded by the current study, however. After being presented with a *T. torosa*, jays were markedly slower to make contact with the presumed mimic, *E. e. xanthoptica*, than with a more cryptically colored subspecies *E. e. oregonensis* (Fig. 2B). In addition, *E. e. xanthoptica* was not eaten in half of the trials, whereas *E. e. oregonensis* was eaten 9 of 10 times.

These results support the hypothesis that the coloration of *E. e. xanthoptica* effectively mimics the aposematic coloration of *Taricha*. In our experiment, however, all the Western Scrub-Jays were first presented with a model species, *T. torosa*, to provide a standardized prior exposure. A definitive test of the mimicry hypothesis requires that predators naïve to the model species be included to eliminate the possibility that elements of the *E. e. xanthoptica* color pattern do not in themselves deter predation. This should be a focus of future research efforts. One would anticipate, however, that aposematic coloration that is neither mimetic nor indicative of noxious or hazardous properties would not consistently deter predators.

Indeed, the results of our feeding trials suggest that the mimetic relationship is Batesian rather than Müllerian. *Ensatina* salamanders possess an abundance of granular glands, particularly in their tails, that produce a milky, glutinous secretion with an astringent taste (S. R. Kuchta, pers. obs.). These secretions are thought to provide a defense against predators (Arnold 1982; Beneski 1982; Hubbard 1903), but prior to this study it was not clear whether these secretions were sufficiently noxious to deter predation by avian predators (Kuchta 2005). In 17 of the feeding trials (10 *E. e. oregonensis* and 7 *E. e. xanthoptica*) the *Ensatina* was consumed by the jay, including the tail in most instances (dead *Ensatina* readily exude secretions following mechanical stimulation). The salamanders were generally consumed with relish, and

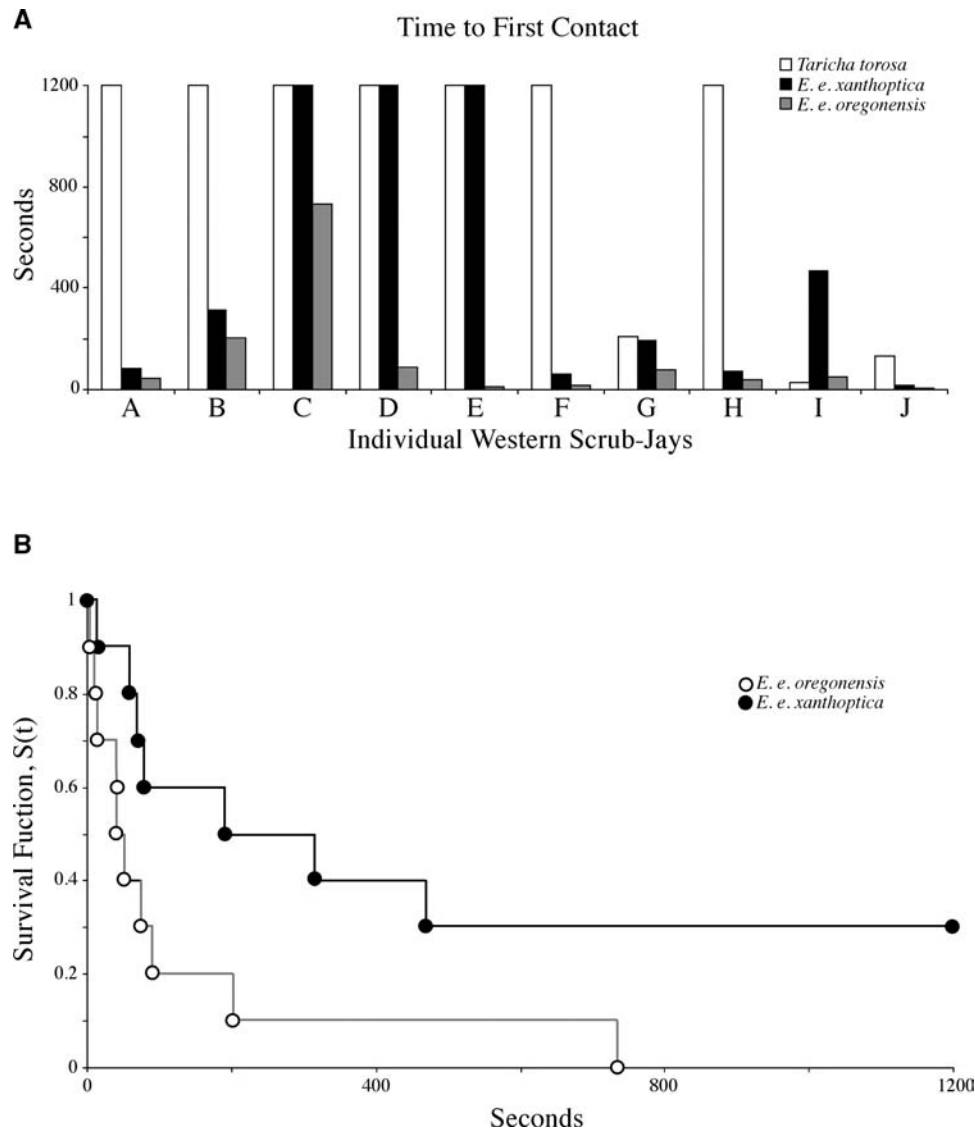


Figure 2. (A) Time to first contact by individual Western Scrub-Jays on all three salamander subjects (*Taricha torosa*, *Ensatina eschscholtzii xanthoptica*, and *E. e. oregonensis*). (B) Survival curves showing the estimated survival probability of *E. e. oregonensis* and *E. e. xanthoptica* as a function of time (sec). 1200 sec = 20 min. The survival curves are significantly different (log-rank test; $P = 0.0299$).

no birds were observed to become ill or behave abnormally after eating an *Ensatina*. Consequently, with regard to avian predators, this suggests that the mimicry of *Taricha* by *E. e. xanthoptica* is an instance of Batesian mimicry, in that *E. e. xanthoptica* is parasitic on *Taricha* from the standpoint of predator learning. This may be true for nonavian predators as well, as a number of amphibians, snakes, and mammals have been recorded to eat *Ensatina* (for discussions of known predators, see Beneski 1982; Kuchta 2005).

Nonetheless, under conditions in which predators are highly motivated to eat, noxious species may be consumed by predators when they would not otherwise be eaten (reviewed in Ruxton et al. 2004). A mimetic relationship between two species may thus be mutualistic (Müllerian) or parasitic (Batesian) depending on the ecological circumstances. Speed (1993) referred to such

a situation as quasi-Batesian mimicry. In our experiment, it did not appear that the avian predators were ever very hungry. It was not possible to prevent the jays from making food stashes in their cages, and jays that did not eat an *Ensatina* were not observed to eat immediately after normal food was returned to their cages. This suggests that the *Ensatina* salamanders eaten in our feeding trials were perceived as edible by the avian predators, and the mimetic relationship between *E. e. xanthoptica* and *Taricha* therefore does not appear to be quasi-Batesian. In addition, *Ensatina* salamanders do not cluster together, and the consumption of an *Ensatina* by an avian predator would be an isolated event. Avian predators will thus not satiate on the toxins of *Ensatina* salamanders, for example, in the manner that they satiate on Monarch butterflies (*Danaus plexippus*) (Brower 1988).

Whether the two subspecies of *Ensatina* salamanders used in the current study, *E. e. xanthoptica* and *E. e. oregonensis*, differ in their relative palatability is not known, though both subspecies were eaten by the jays in our feeding trials. Study of the properties of the secretions produced by *Ensatina*, including patterns of geographic variation and differentiation among subspecies, would benefit the analysis of adaptive differentiation in the complex (e.g., Fontana et al. 2006). The extremely glutinous secretions exuded by *Ensatina* may function primarily as an adhesive, as opposed to a noxious, defense. For example, Arnold (1982; S. J. Arnold, pers. comm.) reported that *E. eschscholtzii* were capable of thwarting ingestion by terrestrial garter snakes (*Thamnophis elegans*) by virtue of the adhesive properties of their secretions. In the current study, we observed that Western Scrub-Jays took from 1:02 to 7:35 min to eat a single tail, and always invested considerable effort scraping their beaks on substrates in the cage during and after feeding.

Newts in the genus *Taricha* are ideal models for a salamander mimicry system because of their extreme toxicity (e.g., Brodie et al. 2005), aposematic coloration (Johnson et al. 1975), and conspicuous, diurnal activity. Avian predators are likely to encounter species of *Taricha* far more often than *Ensatina*, which are nocturnal and secretive in nature (see discussion in Kuchta 2005). Within *Taricha*, there is geographic variation in the relative levels of toxicity among individuals and populations, with individuals in some populations likely palatable, and individuals in other populations absolutely lethal to most predators (Brodie et al. 2005, and references therein). The extreme level of toxicity found in some populations is thought to be the result of a coevolutionary arms race with garter snakes (*Thamnophis sirtalis* and *T. couchii*), which are able to consume newts despite this toxicity (Brodie et al. 2002, 2005). The toxicity of *T. torosa* has not been measured for either of the populations in the current study. Published research indicates that populations in the San Francisco Bay region are of relatively high toxicity (Brodie et al. 2002), but levels of toxicity may in fact vary on a finer-scale than this (E. D. Brodie, Jr., pers. comm.). It is important to distinguish between the levels of toxicity that *Thamnophis* would find problematic, because these predators have evolved resistance to TTX (Geffeney et al. 2005), and the levels of toxicity that an avian predator would find noxious. In the current study, 17 of 20 *Ensatina* were eaten, yet none of the *T. torosa* were consumed, indicating the jays did not consider *T. torosa* palatable.

The results of the current study, which support a mimetic relationship between *E. e. xanthoptica* and *Taricha*, have implications for ongoing studies of diversification in the *Ensatina* complex. *Ensatina eschscholtzii* is a polytypic species with multiple geographically discrete color morphs, and studies of the biogeography of diversification in the *Ensatina* complex have made this species a noted example of a "ring species" (Stebbins 1949; Wake 2006).

The subspecies *E. e. xanthoptica* is a fundamental player in the *E. eschscholtzii* ring species scenario because it occupies a central position in the ring, forming secondary contacts with the subspecies *E. e. oregonensis* and *E. e. eschscholtzii* in central coastal California (Wake 1997) and *E. e. platensis* in the foothills of the Sierra Nevada Mountains (Wake et al. 1989; Alexandrino et al. 2005). The subspecies *E. e. oregonensis* and *E. e. eschscholtzii* are postulated to be cryptic by way of background matching (Stebbins 1949), whereas *E. e. platensis* is thought to be cryptic by way of disruptive coloration (Stebbins 1949). Thus, where different subspecies come together, there may be selection against hybrid individuals because such hybrids will possess an intermediate phenotype (e.g., Mallet et al. 1990; Langham 2004; Sinervo and Calsbeek 2006). For example, hybrids between *E. e. xanthoptica* and *E. e. platensis* are not effective mimics of *Taricha*, nor are they disruptively colored, and it has been postulated that predator-mediated selection against hybrid phenotypes contributes to the maintenance of the narrow hybrid zone between these two subspecies (Wake et al. 1989; Alexandrino et al. 2005). A similar scenario may be found in the San Francisco Bay area between *E. e. xanthoptica* and *E. e. oregonensis*, but this requires more study (Wake 1997). Empirical analysis of the ecological function of the phenotypes found in the *Ensatina* complex is thus important for evaluating the ring species hypothesis because of its relationship to hybrid fitness at points of secondary contact (Wake 1997, 2006).

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