

is no evidence of any local extinctions on Whitetop Mountain, Mt. Rogers, Beech Mountain, Bluff Mountain, or Pine Mountain in Virginia during the last half of the twentieth century (Organ, 1993, and personal communication). Organ's findings were based on intensive quantitative sampling in the Mt. Rogers National Recreational Area in the late 1950s, the late 1960s, 1970, and again in 1989–92. All the known Virginia localities for the species are situated within the Mt. Rogers Recreational Area, Jefferson National Forest (Mitchell and Reay, 1999).

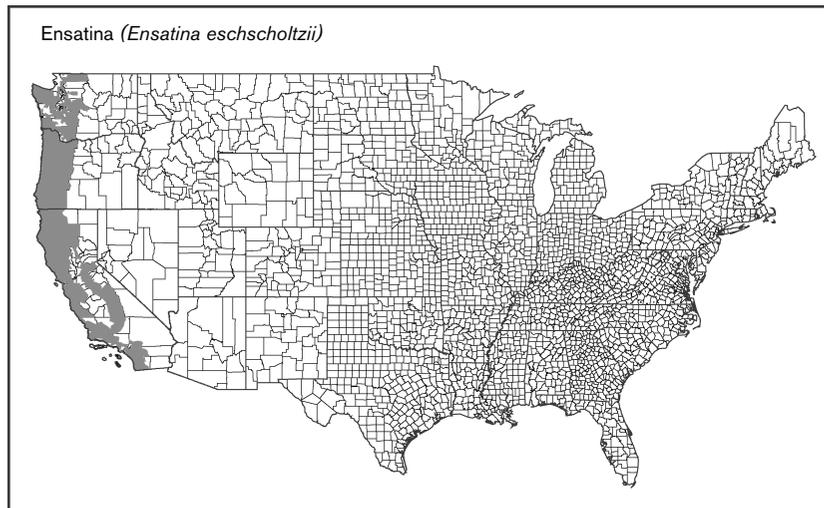
Based on her recent and extensive experience with pigmy salamanders in the field, Erica Crespi (personal communication) observed that in the Great Smoky Mountains, Plott Balsams, Great Balsams, and southward, populations of pigmy salamanders were patchy in distribution, but that enough of them exist to provide long-term stability. In that part of the range, individuals were abundant in small patches (approximately 20 m × 50 m²), but such patches were difficult to find. In contrast, Crespi noted that the more northern populations of the species (Mt. Rogers, Whitetop Mountain, Roan Mountain, and Grandfather Mountain) are more isolated from one another and exist in fewer patches that are farther apart. In that area, pigmy salamanders were locally common in small patches, but patches were uncommon or rare. Thus, northern populations may be more vulnerable to extinction in the face of environmental change.

Ensatina eschscholtzii Gray, 1850
ENSATINA

Shawn R. Kuchta, Duncan Parks

1. Historical versus Current Distribution.

Ensatinas (*Ensatina eschscholtzii*) have the widest distribution of any West Coast plethodontid, ranging from the central coast of British Columbia and Vancouver Island, Canada (Kelson et al., 1999), to northern Baja California, Mexico (Mahrtdt, 1975; Stebbins, 1985). Seven morphologically distinct subspecies—painted salamanders (*E. e. picta*), Oregon salamanders (*E. e. oregonensis*), yellow-eyed salamanders (*E. e. xanthoptica*), Monterey salamanders (*E. e. eschscholtzii*), Sierra Nevada salamanders (*E. e. platensis*), yellow-blotched salamanders (*E. e. croceater*), and large-blotched salamanders (*E. e. klauberi*)—are arranged parapatrically in a ring around the Central Valley of California (Stebbins, 1949b, 1985). Monterey salamanders (coastal) and large-blotched salamanders (inland) are locally sympatric at four sites in southern California, with little or no hybridization (Brown and Stebbins, 1964; Stebbins, 1957; Wake et al., 1986), yet intergradation occurs between geographically adjacent subspecies in a loop around the Central Valley of California. Thus, *Ensatina eschscholtzii* is



usually considered a ring species (Stebbins, 1949b; for recent studies of the ring species issue, see Wake et al., 1986; Wake and Yanev, 1986; Wake et al., 1989; Moritz et al., 1992; Jackman and Wake, 1994; Wake, 1997; Highton, 1998; Wake and Schneider, 1998). A second ring is completed in the Sierra Nevada where yellow-eyed salamanders and Sierra Nevada salamanders hybridize (Wake et al., 1989). Some researchers consider the complex to be comprised of many distinct species (Highton, 1998), and large-blotched salamanders in particular are sometimes treated as a separate species (Frost and Hillis, 1990; Collins, 1991; Grismer, 1994). Aside from localized extinctions, historical and current distributions appear similar.

2. Historical versus Current Abundance.

Ensatinas usually are common where present. Stebbins (1954b) estimated 1,730 yellow-eyed salamanders/ha in mature redwood forest in Contra Costa County, California. Gnaedinger and Reed (1948) estimated 2,833 Oregon salamanders/ha in a wooded canyon in Multnomah County, Oregon.

In the Tehachapi Mountains, yellow-blotched salamanders are positively associated with canyon live oak (*Quercus chrysolepis*) and negatively associated with blue oak (*Q. douglassii*; Block and Morrison, 1998). Development and the cutting of oak woodland in the Tehachapi Mountains may threaten yellow-blotched salamanders (Jennings and Hayes, 1994a). In Douglas fir forests in northern California, Oregon salamanders are more abundant in old-growth stands than in young or mature stands (Bury, 1983; Raphael, 1988; Welsh and Lind, 1988, 1991). In the industrial, managed forests in the Cascades of Washington, Oregon salamanders are more abundant in rotation age stands (from about 45–70 yr) than in younger stands (Aubry, 2000; Grialou et al., 2000). However, in Washington and

Oregon there is no correlation between stand age and Oregon salamander abundance in unmanaged Douglas fir forests (Aubry et al., 1988; Corn and Bury, 1991; Gilbert and Allwine, 1991). In old-growth Douglas fir forests in northern California, Oregon, and Washington, Oregon salamanders consistently are more abundant in drier sites (Aubry et al., 1988; Aubry and Hall, 1991; Gilbert and Allwine, 1991; Welsh and Lind, 1991). Finally, in managed Douglas fir forests in the Oregon Cascades, Oregon salamander abundance is positively correlated with the volume of coarse woody debris (Butts and McComb, 2000), but this correlation is not found in the Washington Cascades (Aubry, 2000).

Stebbins (1951) has observed that edge habitats support the highest abundances of ensatins and notes that they appear more abundant on flat or gently sloping shelves above flood level than on steep terrain. Storer (1925) stated that yellow-eyed salamanders in central California are less abundant than arboreal salamanders (*Aneides lugubris*), a situation that is now reversed, probably in part because arboreal salamanders are now less common (D. B. Wake, personal communication).

3. Life History Features.

A. Breeding.

Reproduction is terrestrial.

i. Breeding migrations. Ensatins do not migrate and movements generally are limited (Staub et al., 1995). Males have abundant spermatozoa throughout the rainy season (September–April throughout much of the range, but extends into June in the Sierra Nevada and northern parts of the range; in the south, rains may not begin until December). Females with sperm capsules in their vents have been found from November–March (Stebbins, 1951).

ii. Breeding habitat. Females lay eggs after retreating to aestivation sites at the end of the rainy season (Stebbins, 1951, 1954b; Jones and Aubry, 1985).

B. Eggs.

i. Egg deposition sites. Eggs masses are found in dark, moist, insulated habitats, such as under and inside logs, under bark, and inside animal burrows (summarized by Petranka, 1998; Stebbins, 1951, 1954b).

ii. Clutch size. Females lay from 3–25 eggs, but 9–16 are most common (data summarized by Petranka, 1998; Stebbins, 1951, 1954b).

C. Direct Development. Clutches are always attended by the female (Stebbins, 1954b). Under laboratory conditions, Collazo (1990) observed that most animals laid eggs in April and May. He monitored the development of five *E. eschscholtzii* clutches to hatching: painted salamander eggs took 113–119 d to hatch (5 eggs), Monterey salamander eggs took 177 d to hatch (4 eggs), and eggs from two Oregon salamander clutches took about 137–142 d (5 eggs) and 129 d (2 eggs), respectively. Time to hatching was negatively correlated with egg size.

D. Juvenile Habitat. Same as adult habitat.

E. Adult Habitat. Ensatinas typically inhabit coniferous forest, deciduous forest, oak woodland, coastal sage scrub, and chaparral (Stebbins, 1951). Individuals are found in thermally buffered, mesic microclimates, such as under logs, bark, and moss (Aubry et al., 1988; Bury and Corn, 1988b; Aubry and Hall, 1991; Corn and Bury, 1991; Gilbert and Allwine, 1991; Welsh and Lind, 1991), under leaf litter (Corn and Bury, 1991), in talus (Herrington, 1988), and in animal burrows (Storer, 1925). They quickly dehydrate on dry substrates (Cohen, 1952) and prefer moist, but unsaturated, soils. Recently, ecological and behavioral aspects of water economy have been described (Wisely and Gollightly, 2003). Unlike many Pacific Northwest plethodontid salamanders, Oregon salamanders tend to be more abundant away from streams (McComb et al., 1993a,b). The range of habitats used by southern California ensatinas is greater than previously described by Stebbins (1951), Fisher and Case (1997), and Jennings and Hayes (1994a), but their habitat use and associations are in need of study (D. B. Wake, personal communication).

F. Home Range Size. Stebbins (1954b) estimated from a 122 × 49 m (400 × 160 ft) plot that home ranges had a maximum width of 10–41 m (mean=19.5 m) for males, and 6–23 m (mean=10 m) for females. Males moved about twice as far between recaptures as females, and the movement of young animals was similar to females. Jacqmotte (1992) estimated home ranges from 0.038–2.6 m² on 10 × 10 m plots, but the small plot size may have biased the home range estimate (Staub et al., 1995). Staub et al. (1995) found average distances between captures to be 26.5 m for males and 19.7 m for females in a grid of pit traps (100 × 300 m)

designed to detect long-distance dispersal (minimum detectable trapping distance=7.1 m). The maximum movement was 120 m for males and 61 m for females.

G. Territories. Evidence for marking, recognizing, and defending home areas has been observed in laboratory settings outside of the breeding season, suggesting territoriality (Wiltenmuth, 1996; Wiltenmuth and Nishikawa, 1998).

H. Aestivation/Avoiding Desiccation. Surface activity by ensatinas is highly correlated with surface moisture (Stebbins, 1951, 1954b), and animals are not commonly encountered above ground during the summer dry season. Individuals aestivate in cool, moist areas, such as animal burrows and inside logs. Emerging individuals often appear dehydrated and usually have empty digestive tracts (Stebbins, 1954b).

I. Seasonal Migrations. None.

J. Torpor (Hibernation). Ensatinas retreat from the surface during periods of freezing temperatures but are not known to hibernate (Stebbins, 1954b).

K. Interspecific Associations/Exclusions. Ensatinas co-occur with salamanders in the genera *Ambystoma*, *Aneides*, *Batrachoseps*, *Dicamptodon*, *Plethodon*, and *Taricha* (Stebbins, 1985). In northern California, Oregon salamanders, black salamanders (*Aneides flavipunctatus*), arboreal salamanders, and California slender salamanders (*B. attenuatus*) differ in their mean and maximum prey size, despite considerable prey overlap (Lynch, 1985). Juvenile Oregon salamanders have a relatively broad head and eat larger prey than sympatric plethodontid juveniles, yet adult ensatinas eat smaller prey than arboreal salamanders (Lynch, 1985). Oregon salamanders eat larger prey than sympatric Larch Mountain salamanders (*P. larselli*) and Dunn's salamanders (*P. dunni*; Altig and Brodie, 1971). Both Lynch (1985) and Bury and Martin (1973) conclude that the diet of Oregon salamanders is generalized relative to sympatric California slender salamanders and climbing salamanders (genus *Aneides*).

L. Age/Size at Reproductive Maturity. Three to four years are required to achieve maturity. Males are sexually mature at about 48–55 mm SVL; females are sexually mature at >60 mm SVL (Stebbins, 1954b).

M. Longevity. Stebbins (1954b) estimated the oldest animals in his study plot to be >8.5 yr, and Staub et al. (1985) estimated ages up to 15 yr.

N. Feeding Behavior. Ensatinas are euryphagous predators of small animals, especially arthropods. Diet is known to include, among others, spiders, mites, beetles, sowbugs, crickets, springtails, centipedes, millipedes, termites, earthworms, and snails (Gnaedinger and Reed, 1948; Zweifel, 1949; Stebbins, 1951, 1954b; Altig and Brodie, 1971; Bury and Martin, 1973;

Lynch, 1985). Most feeding is sit-and-wait ambush, but ensatinas will stalk to get within range of prey items once they are spotted. The functional morphology of prey capture behavior is a stereotyped protrusion of the hyomandibular apparatus and partially attached tongue; timing and magnitude of tongue and jaw movements are modulated prior to protrusion to accommodate distance, prey type, and other factors (Deban, 1997).

O. Predators. Known predators include Stellar's Jays (*Cyanocitta cristata*; Stebbins, 1954b), garter snakes (*Thamnophis* sp.; Fitch, 1940; Beneski, 1989), and raccoons (*Procyon lotor*; Wake et al., 1989). Stebbins (1954b) discusses other possible predators.

P. Anti-Predator Mechanisms. Harassed ensatinas stand on their toes stiff-legged, arch their back down, hold the neck erect with the head horizontal or downward, and arch and flip their tails in the direction of the attacker (Stebbins, 1951; Brodie, 1977). The dorsal surface of ensatina tails contains large, densely packed poison glands, and a sticky, milky secretion is exuded when the animal is threatened (Hubbard, 1903). Ensatinas can autotomize their tails at the constricted base, and autotomized tails bend wildly for several minutes (Stebbins, 1954b; Wake and Dresner, 1967). Beneski (1989) found that ensatina tails stick to the mouths of garter snakes, inhibiting further consumption. It takes about 2 yr to regenerate an autotomized tail (Stebbins, 1954b; Staub et al., 1985), and tails are rarely dropped unless conditions are life threatening (Beneski, 1989). Rarely, threatened ensatinas will vocalize with a hissing sound, similar to a snake (Stebbins, 1951; Brodie, 1978). Yellow-eyed salamanders are probably Mullerian mimics of the extremely toxic newts of the genus *Taricha* (Stebbins, 1949b; C. W. Brown, 1974; Wake et al., 1989; Kuchta, 2002).

Q. Diseases. Unknown.

R. Parasites. Helfer (1949), Lehmann (1954), and Goldberg et al. (1998c) examined the helminth communities in ensatinas. Two cestode and two nematode species were documented. Of 30 ensatinas from Del Norte and Humboldt counties, California (within the range of painted salamanders and Oregon salamanders), Goldberg et al. (1998c) found 17 contained at least one species of parasitic helminth (average number of helminth species/infected salamander = 1.1 ± 0.3). They concluded that the helminth infracommunities of ensatinas are depauperate relative to other vertebrates. The effect of parasites on ensatina fitness or ecology has not been examined.

4. Conservation.

Ensatinas usually are common where present. In Douglas fir forests in northern California, Oregon salamanders are more

abundant in old-growth stands than in young or mature stands and are consistently more abundant in drier sites (see "Historical versus Current Abundance" above). In the industrial, managed forests in the Cascades of Washington, Oregon salamanders are more abundant in rotation-age stands from about 45–70 yr than in younger stands. However, in Washington and Oregon there is no correlation between stand age and Oregon salamander abundance in unmanaged Douglas fir forests (see "Historical versus Current Abundance" above).

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Eurycea aquatica Rose and Bush, 1963
DARK-SIDED SALAMANDER

Kenneth H. Kozak, Michael J. Lannoo

1. Historical versus Current Distribution.

Rose and Bush (1963) and Jones (1980) reported dark-sided salamanders (*Eurycea aquatica*) from small springs in the Ridge and Valley Physiographic Province of Alabama (Jefferson, Shelby, and Saint Clair counties) and northwestern Georgia (Catoosa, Chattooga, Floyd, Gordon, Murray, Walker, and Whitfield counties). They appear to be absent south of the Coosa River despite the availability of suitable spring habitats (Jones, 1980). Ashton (1966) reported specimens matching the description of dark-sided salamanders from Davidson County, Tennessee, in the Interior Low Plateaus Physiographic Province.

The species status of *E. aquatica* is controversial. Mount (1975) examined dark-sided salamanders from Alabama and found many individuals intermediate in morphology between southern two-lined salamanders (*E. cirrigera*) and dark-sided salamanders; he therefore considered these two taxa conspecific. Similarly, Jones (1980) conducted a comprehensive morphological study of the *E. bislineata* complex in the Ridge and Valley Province of Alabama and Georgia. At many of the examined localities, "intermediates" between southern two-lined salamanders and dark-sided salamanders were found, which Jones (1980) also interpreted as evidence of hybridization. Both Mount (1975) and Jones (1980) considered dark-sided salamanders to represent a "spring ecotype" of southern two-lined salamanders rather than a distinct species. Jacobs (1987) studied allozyme variation in the *E. bislineata* complex and found *E. aquatica* from the type locality in Jefferson County, Alabama, to be similar to Junaluska salamanders (*E. junaluska*) and some populations of *E. cirrigera*. Similarly, Wallace (1975) found that individuals possessing morphological characteristics of *E. aquatica* and *E. cirrigera* were genetically indistinguishable.

Redmond and Scott (1996) follow Wallace (1975) and place *E. aquatica* in Tennessee in synonymy with *E. cirrigera*. However, the status of *E. aquatica* in Alabama and Georgia remains controversial. Petranka (1998) considers *E. aquatica* to be synonymous with *E. cirrigera*, but Sever (1989) states that "the formal decision on the status of *E. aquatica* must await the comprehensive study of the species in Alabama and neighboring areas called for by Mount (1975) and Jones (1980)." Phylogeographic analyses of mtDNA variation

indicate that populations of *E. aquatica* from the Ridge and Valley Province in Alabama form a monophyletic group that is divergent from any recognized species in the *E. bislineata* complex (Kozak and Larson, in preparation). This result corroborates Jacob's (1987) allozyme data indicating that *E. aquatica* from the type locality are genetically distinct from populations of *E. cirrigera* in Alabama, Georgia, and Tennessee. Thus, *E. aquatica* from the Ridge and Valley Province of Alabama should be considered an evolutionary unique lineage that warrants conservation (Moritz, 1999).

au: update?

2. Historical versus Current Abundance.

Unknown. Rose (1971) states: "The springs in the area of the type locality of *Eurycea aquatica* are very small, and transformed animals in this area are nonexistent. Wholesale destruction of the springs was hastened by the discovery of endemic fish in the area and undisciplined herpetological collecting."

3. Life History Features.

Many aspects of the life history of dark-sided salamanders have not been described. Refer to the *Eurycea cirrigera* (Pauley, this volume) and *E. bislineata* (northern two-lined salamanders; Sever, this volume) accounts for information that can be used provisionally until data on dark-sided salamanders can be collected.

A. Breeding.

i. Breeding migrations. Unlikely. During wet periods and at higher altitudes, adults may wander far from breeding areas in springs, seeps, and streams. Dry conditions, however, will cause these animals to return to aquatic habitats. Eggs are laid in water, and larvae are aquatic, so females will congregate at appropriate nesting sites (see species accounts for *Eurycea cirrigera*; Pauley, this volume; and *E. bislineata*; Sever, this volume).

ii. Breeding habitat. Springs and small woodland streams are the most likely nesting sites (Rose and Bush, 1963).

B. Eggs.

i. Egg deposition sites. Eggs are likely deposited on the undersides of rocks and logs in flowing water, and females brood (see Pauley, this volume; Sever, this volume).

ii. Clutch sizes. The average clutch size in the vicinity of the type locality is 80 (range 60–96; Rose and Bush, 1963). Clutch sizes for northern two-lined salamanders and southern two-lined salamanders average from 20–50 (see Pauley, this volume; Sever, this volume), suggesting the reproductive potential of dark-sided salamanders is high relative to other species in the *E. bislineata* complex.

C. Larvae/Metamorphosis. Larvae are aquatic.

i. Length of larval stage. There is typically a bimodal distribution of larval SVLs, suggesting that the larval stage lasts 2 yr. The

