

# Ontogenetic Shift in Habitat Use in the Western Fence Lizard (*Sceloporus occidentalis*) in Northern California

Ontogenetic shifts in habitat use are obvious for many amphibian species where aquatic larvae shift to terrestrial adults. In lizards, where ontogenetic habitat shifts may not be nearly as dramatic as those that accompany amphibian metamorphosis, there is still evidence for important habitat changes during development. Two general patterns have been observed in lizards. Habitat shifts can occur either 1) horizontally, where ontogeny is associated with different habitat types across a landscape or 2) vertically, where a species remains in the same habitat type but shifts its distribution altitudinally along a substrate (e.g., rocks or trees).

Horizontal shifts have been observed in several lizard species. In *Anolis aeneus*, Stamps (1983) found that juveniles hatch in shady areas, migrate to clearings, and then move back into

shady habitat as adults. Hirth (1963) observed that *Basiliscus plumifrons* juveniles are most commonly found on beaches

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whereas adults of the species are found almost exclusively in adjacent hedges. Baharav (1975) found that young *Phrynosoma solare* remained adjacent to ant nests whereas adult horned lizards used habitat along ant trails, farther from ant mounds and closer to large rocks used for basking. Another horizontal-type ontogenetic habitat shift has been observed in the agamid, *Amphibolurus ornatus*, where adults are predominantly found on rock outcroppings whereas juveniles are concentrated at the base of boulders adjacent to these outcroppings (Bradshaw 1971).

Vertical habitat shifts are documented in *Iguana iguana* (Henderson 1974), *Anolis cristatellus* (Kiestler et al. 1975), and *Chamaeleo chamaeleon* (Keren-Rotem et al. 2006), where adults are found higher in trees whereas juveniles use the base of trees or remain on the ground. Interestingly, *Varanus komodoensis* exhibit a similar, albeit reversed, pattern where hatchlings are arboreal whereas older animals are terrestrial (Imansyah et al. 2008). In Africa, *Pseudocordylus capensis* exhibits a vertically-stratified distribution where adult males are highest on rocks, adult females are at intermediate heights, and juveniles are found at the base of rocks (Eifler et al. 2007). Simon and Middendorf (1976) found that *Sceloporus jarrovi* shifts from using smaller, lower branches as juveniles to larger, higher branches as adults. Furthermore, although the territories of all *S. jarrovi* age classes spatially overlap, there is a temporal habitat shift where adults use the habitat in the mornings whereas juveniles do so in the afternoon (Simon and Middendorf 1976).

Stamps (1983) outlined six non-mutually exclusive factors that might explain ontogenetic habitat shifts: spatial distribution of food, suitable perches, intraspecific competition with another age class, interspecific competition, thermoregulatory constraints, and predation by conspecifics or other species. Predation pressure best supported the horizontal habitat shift seen in *A. aeneus* (Stamps 1983) and the vertical shift seen in *C. chamaeleon* (Keren-Rotem et al. 2006). There is also support for intraspecific competition (Bradshaw 1971; Schall 1974), food (Baharav 1975; Henderson 1974), and perches (Simon and Middendorf 1976) as explanations for certain ontogenetic habitat shifts in lizards. Although habitat use by different lizard age classes can be potentially complex, understanding habitat use during ontogeny is integral for studying population dynamics and processes (Lecchini and Galzhin 2005).

Our goal in the present study is to determine whether there was a difference in habitat use between two age-classes of Western Fence Lizards (*Sceloporus occidentalis*), young-of-the-year (hereafter juveniles) and adults. We used area- and time-constrained searches to measure adult and juvenile lizard densities in riparian cobble bars as well as upland, grassland habitats in northern California. In our study, riparian cobble bars and grassland habitats are particularly interesting because of their spatial juxtaposition. These cobble bars extend short distances (~2–20 m) from rivers and transition sharply into grassland habitat. The close proximity of these different environs implies that lizards should be able to readily cross between cobble bars and grassland. Given this, we were interested in whether there were differences in habitat use between age classes across relatively short distances. Because of the previously documented riverine subsidies (foreign nutrient inputs from areas of higher productivity into areas of low productivity, Sabo and Power 2002), and thermoregulatory or predatory refuge advantages (Sabo 2003) provided by riparian cobbles, we predicted that juvenile *S. occidentalis* would appear disproportionately more often in riparian

cobble bars relative to adult lizards. We further predicted that adult lizards would be more prevalent in upland habitat farther from the stream edge where they could potentially capitalize on different thermoregulatory substrate and prey resources. Although *S. occidentalis* is widespread and is heavily studied, to our knowledge there has been no evaluation of an ontogenetic habitat shift in this species. Here, we provide the first evidence of differential habitat use between juvenile and adult *S. occidentalis*. Because habitat management is key in wildlife conservation, understanding age-specific habitat use is important for management.

**Materials and Methods.**—Our study took place adjacent to the confluence of the South Fork Eel River and Fox Creek in the Angelo Coast Range Reserve (Mendocino Co., California, USA) during September 2010. We focused on a riparian cobble bar and its adjacent upland, grassland habitat (Fig. 1). For each habitat type (riparian and upland), we selected two habitat patches that were neighboring each other, resulting in four adjacent survey sites.

For surveys, we selected two riparian and two upland sites and conducted a half-hour time-constrained search at each location. We surveyed one pair of riparian and upland sites over two consecutive days and then surveyed the other two sites (one upland and one riparian) on the following two days. We confined our surveys visually using physiognomic delineations between the surveyed habitat and adjacent habitats (i.e., hard transitions from cobble to grassland, dirt paths, trees, etc.). The two upland habitat patches were 2,042.5 m<sup>2</sup> and 409 m<sup>2</sup>, while the two riparian sites were 441 m<sup>2</sup> and 387.2 m<sup>2</sup> in size. Because the home range size of *S. occidentalis* is approximately 19–50 m<sup>2</sup> for juveniles and 51–73 m<sup>2</sup> for adults (Davis and Ford 1983), and because all sites were less than 10 m apart, we pooled the two replicate sites for both habitat types for statistical analysis, assuming some movement of lizards among habitat patches. In order to avoid straying into adjacent habitat we surveyed approximately 1 m inside of edges. Each time we spotted a lizard we would pause the search effort and capture the lizard. We captured adult lizards using a noose made from a fly-rod and dental floss and captured juveniles either by noose or a dip net. Although lizards seldom evaded capture, if a lizard escaped, we restarted the search effort. The same two surveyors were responsible for sighting and capturing all lizards. One surveyor was responsible for net captures while the other was responsible for noose captures. On the ventral side of each lizard, we used a felt-tipped pen to write a unique three-digit number and then measured its snout-vent length (SVL). As in Lambert et al. (2012), *S. occidentalis* exhibited a bimodal distribution of SVLs in which juveniles all had an SVL < 4 cm and adults had SVLs > 5 cm, with no individuals between these two size classes. After we processed and released lizards, we continued the search where we had stopped previously. On the following day, we resurveyed the same areas but in reverse order so that each location was surveyed once in the morning and once in the evening. This is important because Simon and Middendorf (1976) found that *S. jarrovi* adults and juveniles temporally segregate in the same habitat, so it is necessary to survey both in the morning and also in the afternoon to adequately assess the number of lizards present. To avoid double-counting individuals, we marked all new individuals captured on the second day of surveys.

We used a Chi-square test to determine whether densities of lizards in the two age classes were distributed non-randomly in the two habitats. We measured the area of each survey site and

calculated lizard densities as lizards/ha. Chi-square tests require integers so we rounded all densities to the nearest integer for analysis.

To characterize the habitats, we randomly oriented two 20-m line-transects that were parallel and spaced 20 m apart in each surveyed area. Every meter, we noted the substrate under the transect line. We defined cobbles as any rock < 0.5 m in length, boulders as any rock > 1 m long, and also identified the dominant substrate such as dry grass or logs.

**Results.**—Including search time as well as lizard processing time, we spent 73–170 minutes (mean = 109.5 min, SD  $\pm$  42.4 min) and 65–148 minutes (mean = 109.75 min, SD  $\pm$  35.7 min) surveying riparian and grassland habitats respectively. In total, we caught 9 adults and 18 juveniles in the riparian habitats and 16 adults and 9 juveniles in the upland habitats. The density of adults was 108.7 lizards/ha in riparian areas and 65.3 lizards/ha in upland habitat. The density of juveniles was 217.3 lizards/ha in riparian areas and 36.7 lizards/ha in upland habitat (Fig. 2). A Chi-square test on the density of lizards indicated a significantly non-random distribution of age classes among two habitat types, such that juveniles were more abundant in riparian areas whereas adults were more abundant in upland areas ( $p < 0.001$ ). Because we marked each animal, we were able to confirm that no animals moved between any of the four study sites.

Our transects indicated that riparian habitat was composed of 48% cobble, 18% sand, 16% live grass, 9% bare ground, and < 3% each of boulders, logs, water, bedrock, and dry grass. Upland habitat was composed of 68% dry grass, 13% cobbles, 6% boulders, and 4% thistle, and < 3% each of logs, live grass, bare ground, manzanita (*Arctostaphylos* spp.), and oak (*Quercus* spp.).

**Discussion.**—Our data provide evidence for an ontogenetic habitat shift in *S. occidentalis*. Similar to Sabo and Power (2002), we found the densities of lizards in general were higher in riparian cobble bars; however, the distributional pattern we observed at least qualitatively shows that the relative proportions of each class was reversed between the two habitat types. Specifically, the number of juveniles was roughly twice that of adults in riparian cobble bars whereas the opposite was true in upland grassland habitat. Although we are unable to explicitly calculate detection probabilities, we are confident that the ability to detect both age classes was relatively equal in both habitat types. On the cobble bars, where juveniles were most prevalent, adults rarely fled under rocks and were readily visible. In the uplands, the grasses were relatively sparse and so juveniles tended to be easy to see. Because of this, we do not believe that our data were dramatically affected by differences in our ability to detect a particular age class in the two habitats.

Interestingly, the total number of lizards caught was similar between habitats, but the total densities of lizards were much lower in the upland habitat relative to the riparian habitat. This is likely because upland habitat was composed mainly of dry grass and was limited in the number of basking and shelter structures like boulders and logs. *S. occidentalis* in the upland habitat were found almost entirely on large basking substrates (logs and boulders), indicating that the species only uses a small fraction of the available habitat. Although the riparian habitats were also limited, and more so, in large basking objects, the main habitat characteristic were cobbles, which can act as refuges, thermoregulatory



FIG. 1. A map showing approximate locations of the riparian (solid line) and upland grassland (dashed line) patches. The study site was along the Eel River at the Angelo Coast Range Reserve, Mendocino, California, USA.

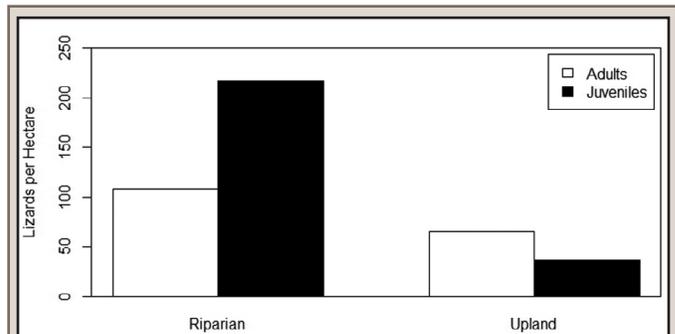


FIG. 2. The densities of adult and juvenile lizards between riparian and upland habitats.

substrate, and high ground for juvenile lizards. Cobbles are also homogeneously distributed in our riparian sites and therefore likely host more lizards for a given unit of area.

Prior work by Sabo and Power (2002) and Sabo (2003) in the same riparian cobble bar system provides inference as to the mechanisms behind this ontogenetic habitat shift. In relation to the hypotheses proposed by Stamps (1983), there is support for food availability, thermal requirements, predation, and appropriate perches. Sabo and Power (2002) found that riverine subsidies in northern California increase growth rates of subadult *S. occidentalis*, suggesting juvenile *S. occidentalis* may be capitalizing on the abundance of invertebrates along cobble bars to accelerate growth when young. Sabo (2003) found that cobbles, relative to other cover like wood or burrows, remained within a more thermally optimal zone for *S. occidentalis* and that gravid female *S. occidentalis* in cobble bars almost exclusively used cobbles for overnight refuge, whereas males were less selective in cobble bars, and upland females relied more on wood and burrows while gravid. Together with our findings, this indicates that cobble bars may provide more thermally ideal habitat for gravid lizards to lay eggs, and that juvenile lizards remain on cobble bars after hatching rather than dispersing as other species of lizards often do (Schall 1974, Stamps 1983). Sabo (2003) also reported predation by garter snakes (*Thamnophis elegans*) on adult female, but not adult male, *S.*

*occidentalis*, and that females choose cobbles that are slightly smaller than those most ideal thermally, suggesting that *S. occidentalis* can preferentially select certain cobbles that are less accessible to larger predators. It is thus possible that juvenile lizards may have more refuge from predators in a riparian cobble bar than in upland areas. Furthermore, larger basking surfaces were more prevalent in the upland habitat relative to riparian habitat, so there may have been inappropriate perches for adult lizards to bask upon in the cobble bars, especially given that it is common for adult lizards to bask higher up than juveniles (Bradshaw 1971; Keren-Rotem et al. 2006; Kiestler et al. 1975). Alternatively, we suggest that adults may defend perches from younger lizards, thus confining juveniles to riparian areas (*sensu* Schall 1974, Schoener 1975).

*Sceloporus occidentalis* is widely distributed in the western United States and occurs in an array of habitats that vary significantly from the riparian cobble bar and upland habitats we studied in northern California (Stebbins 2003). Asbury and Adolph (2007) found that *S. occidentalis* from geographically separated and distinct habitats exhibit a high degree of behavioral plasticity and tend to choose similar basking structures when placed in similar environments. We recommend future investigation as to whether *S. occidentalis* exhibits ontogenetic habitat shifts across a wider array of habitat types and, if they do, which factors (e.g., food or thermoregulation) drive this habitat shift. From an evolutionary ecology perspective, this could be particularly interesting in novel, urbanized settings where *S. occidentalis* not only occurs (Asbury and Adolph 2007), but where its physiology and ecology might have changed over time, potentially in favor of greater juvenile growth and survival.

Given how widespread, common, and heavily studied *S. occidentalis* is, it surprises us that an ontogenetic habitat shift has not yet been reported for this species. If these habitat shifts occur commonly in wildlife, as the literature indicates for lizards, then understanding such patterns may be important for managing the appropriate habitat features for species of conservation concern. We believe this study highlights the importance of studying the habitat use of different age classes across species.

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