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## **Resource Partitioning in Two Stream Salamanders, *Dicamptodon tenebrosus* and *Rhyacotriton cascadae*, from the Oregon Cascade Mountains**

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## Notes and Discussion

### Resource Partitioning in Two Stream Salamanders, *Dicamptodon tenebrosus* and *Rhyacotriton cascadae*, from the Oregon Cascade Mountains

**ABSTRACT.**—We investigated the potential for resource partitioning between the Coastal giant salamander (*Dicamptodon tenebrosus*) and the Cascade torrent salamander (*Rhyacotriton cascadae*) by examining their diet and microhabitats in forest streams. Larval *D. tenebrosus* and *R. cascadae* fed primarily upon aquatic insect larvae. We found similar foods in larval and adult *R. cascadae* and combined these results. *Dicamptodon* larvae consumed ephemeropteran, plecopteran, and trichopteran larvae in about equal amounts whereas *R. cascadae* ate more trichopteran and less ephemeropteran larvae than *D. tenebrosus*. Diet of all *R. cascadae* overlapped more with smaller than larger sized *D. tenebrosus* larvae. Comparisons of diets with available foods indicated *R. cascadae* is more selective or more gape-limited in its feeding habits than *D. tenebrosus* larvae. The two salamanders differed in use of microhabitats in creeks, which may contribute to their diet differences.

#### INTRODUCTION

Resource partitioning in reptiles and amphibians may result from an interaction of mechanisms including competition, predation, and factors that operate independently of interspecific interactions, such as physiological constraints (Toft, 1985; Shine, 1991; Sih and Christensen, 2001). Salamanders generally partition food with prey size more than food type due to limitation of gape size (see Lynch, 1985). In particular the size-frequency distribution of food available to hatchling salamanders may be the primary selective force in the evolution of reproductive strategies in salamanders (Nussbaum, 1985).

Aquatic amphibians are the predominant vertebrate predators in many smaller streams of western Oregon. Stream amphibian density and biomass are greater than those reported for salmonid fishes (Bury *et al.*, 1991). The Coastal giant salamander, *Dicamptodon tenebrosus*, and the Cascade torrent salamander, *Rhyacotriton cascadae*, often occur together in Oregon Cascades streams (Nussbaum, 1976; Hayes, 2005; Jones and Welsh, 2005). However, they often are in different parts of stream basins. In general *R. cascadae* occur in high gradient reaches, waterfalls or seeps, whereas *D. tenebrosus* are associated with wider streams and often are in pools (Welsh and Lind, 1996; Olson and Weaver, 2007; Welsh, 2011). Larval *D. tenebrosus* attain much greater size than *R. cascadae* larvae (see Good and Wake, 1992) so this may reduce food competition, if it occurs, between the two taxa. Still, smaller *D. tenebrosus* may compete for resources, including food (Toft, 1985; Bury, 1988). Dietary overlap might be expected to be greatest between *R. cascadae* and *D. tenebrosus* larvae of similar size.

Prey items of adult *Rhyacotriton* included amphipods, small snails, worms, springtails, larval flies and stoneflies, and beetles (Bury and Martin, 1967; Bury, 1970; Nussbaum *et al.*, 1983). Although Hayes (2005) and Welsh and Karraker (2005) reported that no data exist on larval food for any of the four species of *Rhyacotriton*, Nussbaum *et al.* (1983) describe larvae feeding on a variety of aquatic invertebrates (but not quantified). Recently, O'Donnell and Richart (2012) reported larval *R. kezeri* consumed a wide variety of invertebrates, including many copepods and flies; whereas, adults fed mostly on arachnids, flies, springtails, and beetles.

Larvae of *D. tenebrosus* feed on a wide variety of aquatic invertebrate (*e.g.*, stoneflies, caddis flies, and mayfly larvae) as well as an occasional small aquatic vertebrates such as fish, tadpoles, and salamander larvae (Johnson and Shreck, 1969; Antonelli *et al.*, 1972; Parker, 1993a). Esselstyn and Wildman (1999) report larval *D. tenebrosus* ( $n = 40$ ) in the Oregon Cascade Mountains had mayflies in highest occurrence in their guts in one stretch of stream and snails (genus *Juga*) in a different stretch.

Although aquatic amphibians are major predators in small Pacific Northwest streams, the roles they perform in aquatic or riparian communities are poorly understood (Bury *et al.*, 1991). Food habits of *D. tenebrosus* and *R. cascadae* in the Cascade Mountains of western Oregon are little quantified nor tested against food availability. Here, we: (1) contrast differences in the diets of both species in two geographic areas; (2) compare stomach contents of salamander larvae with available prey and microhabitat use in one stream; and (3) examine the potential for food competition based on dietary overlap.

TABLE 1.—Specific locations of study streams

Mount Hood National Forest	Willamette National Forest
45.48°N, 122.02861°W	44.225°N, 122.16389°W
45.43°N, 122.17361°W	44.26667°N, 122.17778°W
45.51306°N, 122.03833°W	44.1753°N, 122.4370°W
45.26889°N, 121.93667°W	44.2637°N, 122.1563°W
45.45694°N, 122.10306°W	44.225°N, 122.19167°W
45.49917°N, 121.97083°W	44.11639°N, 122.19972°W

METHODS

STUDY AREAS

We collected salamanders in the Western Hemlock (*Tsuga heterophylla*) Zone of the Western Cascades Physiographic Province (Franklin and Dyrness, 1973). We sampled permanent creeks occurring in mature closed-canopy stands dominated by Douglas-fir (*Pseudotsuga menziesii*) in western Oregon. We sampled six creeks in each of two study areas in Oregon: (1) Mount Hood National Forest, Multnomah and Clackamas counties; and (2) Willamette National Forest, Lane and Linn counties. Specific locations are in Table 1.

SAMPLING PROTOCOL AND HABITAT MEASUREMENTS

We found larval *D. tenebrosus* in approximately equal numbers at each study area, but we caught most larval and adult *R. cascadae* (85%) at Mt. Hood. We sampled 10 m lengths of creeks intensively for salamanders using small hand-held seines and dip nets (see Bury and Corn, 1991). We noted microhabitat of each salamander upon capture: riffle, pool, splash zone or seep. All salamanders were relaxed in MS-222. They then were preserved in 10% buffered formalin immediately after capture and later transferred to 70% ethanol. Specimens were deposited at the Charles R. Conner Museum, Washington State University, Pullman, Washington. Stomach contents were examined in water with the aid of a dissecting microscope and percent volume was visually estimated for each item. We summarize data as percent volume (total percent volume contributed by that item) and percent frequency (percent of stomachs containing that item) separately for large larval (snout-vent length  $\geq 56$  mm) and small larval (SVL  $< 56$  mm) *D. tenebrosus*, larval *R. cascadae*, and adult *R. cascadae*. We employed a maximum SVL of 56 mm for small *D. tenebrosus* larvae because we found no *R. cascadae*  $> 55$  mm SVL. Thirteen of 250 (5.2%) *D. tenebrosus* stomachs and 16 of 131 (12.2%) *R. cascadae* stomachs were empty and were omitted from the analysis.

We sampled Mack Creek, H.J. Andrews Experimental Forest, Oregon, for both salamanders and available food. We collected benthic organisms at 25 randomly placed, 0.1 m<sup>2</sup> quadrats in Mack Creek with a Surber-type bottom sampler. We removed invertebrates from each bottom sample, preserved in 70% ethanol and identified major items to family. We estimated percent volumes for each item in the sample and then summarized data for comparison with stomach content data.

STATISTICAL ANALYSES

We determined dietary overlap between species using the similarity index discussed in Horn (1966), which ranges from no overlap (zero) to complete overlap (1). Values  $> 0.60$  indicate similar diets (Zaret and Rand, 1971). Marshal *et al.* (2012) reported that this index has relatively low bias and is appropriate for studies in which selection of resources is reported as a proportion of total resources used by the animal. Chi-square analyses were used to test for differences among diets and microhabitat use and to compare diets to food availability.

RESULTS

Both large and small *D. tenebrosus* larvae fed primarily on mayfly (Ephemeroptera), stonefly (Plecoptera), and caddis fly (Trichoptera) larvae (Table 2). These prey items accounted for 58.3% of the food volume of large salamander larvae and 71.3% of the volume in small salamanders. The only

TABLE 2.—Percent of foods of large (SVL  $\geq 56$  mm) and small (SVL  $< 56$  mm) *Dicamptodon tenebrosus* larvae and *Rhyacotriton cascadae* from 12 streams in the Oregon Cascade Mountains. V = volume; F = frequency

Food types	<i>Dicamptodon</i>				<i>Rhyacotriton</i>	
	Large (n = 88)		Small (n = 149)		All (n = 115)	
	% V	% F	% V	% F	% V	% F
Ephemeroptera						
Ephemerellidae	2.1	6.8	1.9	4.7	0.6	2.6
Heptageniidae	8.4	46.6	16.9	48.3	1.2	6.1
Leptophlebiidae	4.1	14.8	3.9	12.1	2.6	6.1
Baetidae	8.0	40.9	9.1	37.6	1.8	11.3
Plecoptera						
Chloroperlidae	6.0	33.0	18.9	47.0	14.9	39.1
Peltoperlidae	1.5	9.1	2.4	14.1	2.2	12.2
Perlidae	7.3	18.2	4.2	9.4	0.0	0.0
Perlodidae	0.8	4.5	1.7	7.4	2.4	8.7
Miscellaneous adults	0.6	3.4	0.9	2.7	0.4	0.9
Trichoptera						
Brachycentridae	4.5	26.1	3.0	17.4	3.2	12.2
Hydropsychidae	3.7	9.1	2.3	4.7	7.4	13.0
Leptoceridae	0.6	4.5	0.1	0.7	0.0	0.0
Limnephilidae	4.4	20.4	2.2	10.1	2.0	5.2
Philopotamidae	4.8	27.3	4.2	19.5	31.4	58.3
Polycentropidae	1.5	5.7	0.5	2.0	0.0	0.0
Miscellaneous adults	8.8	20.5	1.8	5.4	1.3	3.5
Diptera						
Chironomidae	2.5	25.0	9.4	55.7	4.5	42.6
Miscellaneous larvae	0.7	2.3	1.3	4.0	0.5	2.6
Miscellaneous adults	1.2	4.5	0.6	2.7	2.8	8.7
Orthoptera (adults)	1.0	2.3	0.2	0.7	0.0	0.0
Coleoptera (adults)	6.6	11.4	1.6	4.7	0.2	0.9
Lepidoptera (adults/larvae)	2.2	4.5	0.3	0.7	0.0	0.0
Hymenoptera						
Miscellaneous adults	1.0	2.3	0.2	0.7	0.0	0.0
Symphyta (larvae)	2.6	9.1	0.4	1.3	0.0	0.0
Shed skin	0.0	0.0	0.0	0.0	1.5	3.5
Ostracoda (Podocopa)	0.2	5.7	3.1	30.2	6.6	32.2
Copepoda Canthocamptidae	0.0	0.0	0.8	4.7	1.7	13.0
Gastropoda Amnicolidae	1.0	6.8	2.5	8.7	4.2	9.6
Aranae	5.5	17.0	3.1	8.7	1.6	7.0
Platyhelminthes ( <i>Dugesia</i> )	0.0	0.0	0.9	2.0	1.8	2.6
Diplopoda (Polydesmida)	3.2	6.8	0.0	0.0	0.0	0.0
Plant ( <i>Pseudotsuga</i> )	2.9	23.9	1.0	5.4	0.9	3.5
Miscellaneous	2.2	11.2	0.5	3.4	1.6	6.9
Totals	99.9		99.9		99.3	

other items contributing more than 3% volume included adult beetles, spiders, and millipedes for large salamander larvae and chironomid larvae, ostracods, and spiders for small salamander larvae. Large salamander larvae fed more on allochthonous (terrestrial in origin) materials (35.6% by volume) than small larvae (10.2%).

Diets of *R. cascadae* larvae and adults did not differ significantly ( $\chi^2 = 7.9$ ,  $P = 0.54$ ,  $df = 9$ ) and were combined (Table 2). They fed heavily upon mayfly, stonefly, and caddis fly larvae (69.7% volume), but in different proportions than *D. tenebrosus* larvae. While *D. tenebrosus* larvae fed on these insect larvae in approximately equal proportions, *R. cascadae* fed much more on caddis fly larvae and less on mayfly larvae than did larval *D. tenebrosus*. Stonefly larvae consumption was similar between the two species. For *R. cascadae*, mayflies (particularly Heptageniidae) were unimportant in the diet, whereas caddis flies of the family Philopotamidae accounted for approximately 30% of total volume. Chironomid larvae, ostracods, and small aquatic snails were also important foods. As with small *D. tenebrosus* larvae, allochthonous materials were relatively unimportant in the diet of *R. cascadae*, accounting for about 10% of total volume.

Patterns in the diets of salamanders collected at Mack Creek were similar to those observed for all samples combined (Table 3). Larval *D. tenebrosus* fed primarily on mayfly, stonefly, and caddis fly larvae in approximately equal amounts while *R. cascadae* fed more heavily on caddis fly larvae. Notable deviations of Mack Creek salamanders from overall diets were the abundance of baetid mayflies and peltoperlid stoneflies in the diets of all salamanders, the abundance of ostracods in the diet of *R. cascadae*, and the absence of small aquatic gastropods in the diets of all salamanders. Baetid mayflies (16.8% volume) and peltoperlid stoneflies (6.1% volume) were abundant in benthic samples (Table 3). Although ostracods did not contribute significantly to total volume of benthic samples (1.2%), they occurred in every sample and usually in high numbers (an average of 42.4 per sample). Small aquatic gastropods did not occur in Mack Creek benthic samples.

Small and large *D. tenebrosus* larvae were most similar in their diets (overlap index = 0.707). The occurrence of allochthonous items such as beetles, spiders, and millipedes in the diet of large larvae accounted for the majority of the difference. Diet of *R. cascadae* yielded overlap index of 0.389 compared to large *D. tenebrosus*, well below 0.60, suggesting dissimilar diets. Overlap index for *Rhyacotriton* and small larval *D. tenebrosus* was 0.503, which indicates some similarities in diet.

Diets of both large and small *D. tenebrosus* larvae at Mack Creek did not differ significantly from available foods as measured by benthic samples ( $\chi^2 = 19.0$ ,  $P = 0.52$ ,  $df = 20$ ,  $\chi^2 = 18.9$ ,  $P = 0.46$ ,  $df = 19$ , respectively), suggesting that they opportunistically take food items in proportion to their availability. In contrast *R. cascadae* diets differed significantly from available foods ( $\chi^2 = 68.3$ ,  $P < 0.01$ ,  $df = 19$ ), indicating that foods are not being taken in proportion to their availability. Further, *R. cascadae* at Mack Creek consumed philopotamid caddis flies and ostracods at levels well above their abundance, and heptageniid mayflies and perlid stoneflies well below their abundance (Table 3).

Analysis of microhabitat use by larval *Dicamptodon* and *Rhyacotriton* at Mack Creek found difference in their use of the four measured microhabitats ( $\chi^2 = 26.0$ ,  $P < 0.01$ ,  $df = 3$ ). Larval *D. tenebrosus* occurred most commonly in pools (49.5% of individuals) and riffles (41.2%) while larvae and adults of *R. cascadae* occurred most commonly in riffles (57.5%) and seepage areas (22.6%) (Fig. 1).

#### DISCUSSION

Larval *D. tenebrosus* feed on a wide variety of prey and appear to consume whatever is most abundant in their habitats (Antonelli *et al.*, 1972; Parker, 1993a; Steele and Brammer, 2006). Similarly, we found opportunistic feeding by larval *D. tenebrosus* because their diets and available foods did not differ significantly. We found many invertebrates but no vertebrate prey in the diets of 237 larval *D. tenebrosus* in the Oregon Cascade Mountains, which was the same pattern found for 362 larvae in the Cascade Mountains of Washington (Steele and Brammer, 2006) and 219 in the Coast Range of Oregon (Graff, 2006).

In contrast to our study, others have shown that larger-sized larval *Dicamptodon* may eat small vertebrates. For example, Johnson and Shreck (1969) reported consumption of larval *Ambystoma gracile* by *D. tenebrosus* and Metter (1963) found tailed frog tadpoles, *Ascaphus montanus*, in stomachs of *D. aterimus*. Antonelli *et al.* (1972) reported trout, *Salmo gairdneri*, and sculpin, *Cottus tenuis*, in the

TABLE 3.—Diets and available foods for *Dicamptodon tenebrosus* and *Rhyacotriton cascadae* collected from Mack Creek, H.J. Andrews Experimental Forest, Lane Co., Oregon. V = volume; F = frequency

Food type	<i>D. tenebrosus</i> (LL)		<i>D. tenebrosus</i> (SL)		<i>R. cascadae</i>		Benthic samples	
	(N = 31)		(N = 39)		(N = 20)		(N = 25)	
	% V	% F	% V	% F	% V	% F	% V	% F
Ephemeroptera								
Ephemerellidae	5.9	19.4	7.4	17.9	0	0	3.6	40
Heptageniidae	6.2	64.5	19.1	71.8	0.3	5	15.6	100
Leptophlebiidae	2.7	16.1	7.6	25.6	1.5	5	2.7	64
Baetidae	16	71	18.5	79.5	9.2	50	16.8	100
Plecoptera								
Chloroperlidae	4.7	35.5	10.1	41	15	50	11.1	100
Peltoperlidae	0.6	12.9	3.3	17.9	7.2	30	6.1	80
Perlidae	3.6	19.4	3	5.1	0	0	8.1	52
Perlodidae	0	0	0	0	0.8	5	0.1	4
Miscellaneous adults	0	0	0	0	2.5	5	0	0
Trichoptera								
Brachycentridae	7.6	35.5	2.3	23.1	3.3	15	4.7	96
Hydropsychidae	1.8	6.5	0.6	2.6	1	5	0.8	8
Leptoceridae	0.5	6.5	0	0	0	0	0.1	4
Limnephilidae	10.4	35.5	3.7	20.5	4	5	13.5	88
Philopotamidae	5.1	45.2	5.1	35.9	29	55	5.2	84
Polycentropidae	3.5	12.9	1	5.1	0	0	1.3	24
Miscellaneous adults	7.5	22.6	0.9	5.1	0	0	0	0
Diptera								
Chironomidae	0.6	12.9	8	59	8.2	60	4.4	100
Miscellaneous larvae	0	0	0.5	2.6	1	5	0.1	4
Miscellaneous adults	0.1	3.2	0.9	2.6	3	5	0	0
Neuroptera								
Corydalidae	0.8	3.2	0	0	0	0	1	4
Coleoptera (adults)	7.7	12.9	0.3	2.6	0	0	0	0
Ostracoda (O. Podocopa)	0.1	6.5	2.8	38.5	13.9	60	1.2	100
Copepoda Canthocamptidae	0	0	0	0	0.1	5	0.2	20.9
Aranae	2.3	6.5	0	0	0	0	0	0
Acarina	0	0	0.1	2.6	0.1	5	1.1	100
Platyhelminthes ( <i>Dugesia</i> )	0	0	3.6	7.7	0	0	1.2	56
Diplopoda (O. Polydesmida)	7.6	16.1	0	0	0	0	0	0
Miscellaneous	2.4	16.1	0.9	7.7	0	0	0.3	12
Totals	99.7		99.7		100.1		99.2	

stomachs of larval *D. tenebrosus*. They stated that all fish were taken during summer low water periods when concentration of fish is greatest in streams. Similarly, Parker (1993) found young-of-year steelhead, *Oncorhynchus mykiss* in larger individuals of larval *D. tenebrosus*. Further, Parker (1994) reported that large (>100 mm TL) larval *D. tenebrosus* had four cases of cannibalism on single young-of-year (<65 mm TL) congeners plus an additional three juvenile trout. As larvae increased in size, they incorporated larger prey into their diet. Esselstyn and Wildman (1999) found two cottid fishes in 40 large-sized larval *D. tenebrosus*. Collectively, these studies include examination of approximately 1877

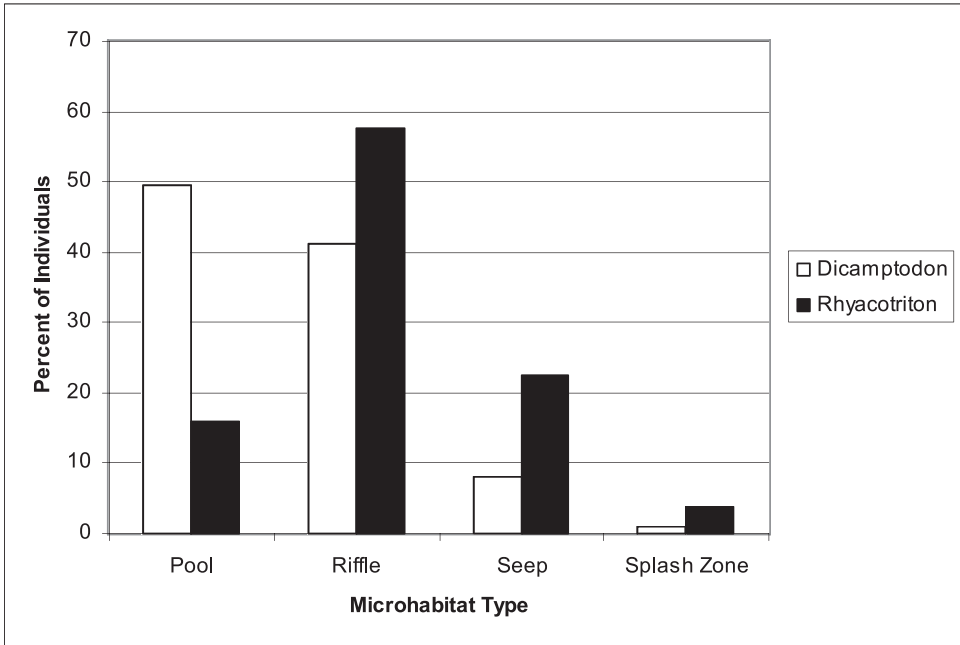


FIG. 1.—Capture locations of *Dicamptodon tenebrosus* (N = 109) and *Rhyacotriton cascadae* (N = 106) in western Oregon creeks

stomachs, and vertebrate prey constitutes only 4% of the diet ( $n = 75$  items) in several species of larval *Dicamptodon*. Thus, range-wide and for all species examined, larger-sized larvae of *Dicamptodon* prey infrequently on some fishes, tailed frog tadpoles, other salamander larvae, and, rarely, smaller congeners. Although infrequent, these items likely provide large amounts of high protein food. Further, capture of small vertebrates appears to occur most often in periods of low water when food items (e.g., fish) are more likely to be confined with salamanders. Although different-sized *Dicamptodon* often occur together in the wild, cannibalism is rare (Bury, 1972; Parker, 1994).

We found small *D. tenebrosus* larvae to be opportunistic and dietary generalists. In contrast diets of *R. cascadae* were not closely tied to available foods where we sampled. There are two possible explanations for this apparent selectivity: (1) *R. cascadae* is more specialized in its feeding habits and has adapted to a more selective feeding strategy or (2) *R. cascadae* occupies slightly different microhabitats than *D. tenebrosus* and food availability in these microhabitats differs from that of the entire stream. Although we had insufficiently detailed measurements to document different microhabitat use by invertebrates, there is some evidence that *D. tenebrosus* and *R. cascadae* are spatially separated in streams (Corn *et al.*, 2003; Welsh and Lind, 1996, 2002). We found that these two species varied in their use of four possible microhabitats with *D. tenebrosus* occurring most commonly in pools and riffles whereas *R. cascadae* frequented riffles, splash zones, and seeps. Bury *et al.* (1991) also described differences in microhabitat use by these species with more *D. tenebrosus* occurring in pools and fewer on wet stream banks and shallow seeps than *Rhyacotriton*.

We found little difference in the diets of larval and adult *R. cascadae*. However, O'Donnell and Richart (2012) reported that larval *R. kezeri* consumed many Copepoda and Diptera whereas adults were feeding mostly on Arachnida, Diptera, Collembola and Coleoptera, which was similar to adult *R. variegatus* in northern California (Bury and Martin, 1967). Overall, there are insufficient studies available to compare geographic or temporal patterns in the four species of *Rhyacotriton*, especially for the larvae.



Although both *D. tenebrosus* and *R. cascadae* feed on a wide variety of the same food items, *D. tenebrosus* is more of a generalist than *R. cascadae*. The two species may be in partial competition by feeding on many of the same items but in different proportions. Differences in food habits, possibly due to the differential use of microhabitats, may contribute to the ability of these two species to co-exist. We found no *R. cascadae* in the diet of *D. tenebrosus*, even when sympatric. This may be partly due to unpalatability of *R. cascadae*: despite being bitten and engulfed, all *R. variegatus* were rejected by *D. tenebrosus* in experimental trials (Rundio and Olson, 2001). However, approximately 25% of the attacked *R. cascadae* did not survive. Thus, avoidance of large larval *Dicamptodon* would be advantageous to the persistence of *Rhyacotriton*.

Aquatic amphibian larvae generally partition season of activity before habitat or foods (Toft, 1985). However, most studies have examined anuran rather than salamander larvae and few have investigated food partitioning directly. We do not know if *R. cascadae* and *D. tenebrosus* larvae are feeding at different times of day. In northern California, both *R. variegatus* and *D. tenebrosus* are active at night (Ashton *et al.* 2006). There is apparently no difference in seasonal use of creeks by larvae. *Rhyacotriton* spends its entire life cycle in seeps, headwaters, or splash zones (Nussbaum and Tait, 1977), while *Dicamptodon* larvae spend 1–3 y as larvae in streams (Nussbaum and Clothier, 1973). Some adult *Dicamptodon* remain in water as neotenes. Resource partitioning by these aquatic salamander larvae seems to follow the general pattern in which food and habitat are partitioned first.

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