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Antipredator Defenses of Larval Pacific Giant Salamanders (*Dicamptodon tenebrosus*) against Cutthroat Trout (*Oncorhynchus clarki*)

DAVID E. RUNDIO AND DEANNA H. OLSON

We tested larval Pacific giant salamanders (*Dicamptodon tenebrosus*) for chemical and behavioral defenses against cutthroat trout (*Oncorhynchus clarki*). Young-of-year *Dicamptodon* were fully palatable to trout during single and repeated offerings. However, larvae increased refuge use in response to chemical cues from trout, although they did not select different microhabitats (shallow or deep) between trout treatments and controls. Our results suggest that, although *Dicamptodon* larvae are potentially vulnerable to predation by cutthroat trout, increased refuge use by larvae in response to trout chemical cues may reduce the probability of encounters and contribute to the coexistence of these species.

AMPHIBIANS have a variety of defenses against predators, including behavioral (e.g., reduced activity level or altered habitat use) and chemical (e.g., unpalatability) mechanisms (Duellman and Trueb, 1986). Both types of defenses may increase survival (Brodie et al. 1978; Resetarits, 1991) and influence the distributions of amphibians relative to predators (Werner and McPeek, 1994). Species that have either type of defense commonly coexist with predators, whereas species lacking defenses generally do not (Azevedo-Ramos and Magnusson, 1999; Kats et al., 1988; Petranka, 1983).

Antipredator defenses appear to be important in mediating predator-prey interactions involving stream amphibians in the U.S. Pacific Northwest (Feminella and Hawkins, 1994; Rundio and Olson, 2001). For example, tailed frog tadpoles (*Ascaphus truei*) reduce foraging activity in response to nonvisual cues from cutthroat trout (*Oncorhynchus clarki*) and Pacific giant salamanders (*Dicamptodon tenebrosus*; Feminella and Hawkins, 1994), and larval southern torrent salamanders (*Rhyacotriton variegatus*) are unpalatable to Pacific giant salamander larvae (Rundio and Olson, 2001). Pacific giant salamanders often are the most abundant species in these headwater assemblages (Hawkins et al. 1983), and although their role as a predator has been examined (Feminella and Hawkins, 1994; Parker, 1994; Rundio and Olson, 2001), little is known about interactions in which this species is a prey.

We investigated defenses of Pacific giant salamander larvae against coastal cutthroat trout (*Oncorhynchus clarki clarki*). These species are abundant in many forested headwater streams where they are the top predators (Hawkins et al., 1983; Murphy et al., 1981). *Dicamptodon* spend 2+ years as aquatic larvae (Nussbaum and Clothier, 1973), and young-of-year larvae

may be prey for trout (Parker, 1992). Larvae are nocturnal, spending the day under cover objects and emerging at night to feed (Nussbaum et al., 1983; Parker, 1994). In headwater streams, *Dicamptodon* are abundant in both riffle and pool habitats at depths from 1 to > 50 cm, although young larvae occur most often in microhabitats < 20 cm deep (DHO, unpubl. data).

Our objective was to test young-of-year *Dicamptodon* for both chemical and behavioral defenses against cutthroat trout. Adult and older *Dicamptodon* larvae produce noxious skin secretions (Nussbaum et al., 1983), but it is not known whether this defense is developed in young-of-year larvae. We tested palatability during both single and repeated offerings to trout because some fishes immediately reject unpalatable prey, but others learn to avoid unpalatable prey after several predation attempts (Crossland, 2001; Kruse and Stone, 1984). Next, we tested whether larvae increase refuge use in response to nonvisual, chemical cues from trout. Nonvisual cues are ubiquitous in aquatic systems (Dodson et al., 1994; Kats and Dill, 1998), and we suspected that they might be important to *Dicamptodon* because larvae are nocturnal. Nocturnal activity alone probably is insufficient defense because trout commonly are active at night (Grunbaum, 1996; pers. obs.). Several species of stream salamanders from the eastern United States increase refuge use in response to fish cues (Kats et al., 1988; Petranka et al., 1987). Finally, we tested whether larvae select shallower microhabitats in response to trout chemical cues. Large cutthroat trout occur primarily in deeper pool habitats in streams (Bisson et al., 1988), and other salamander larvae shift to shallower microhabitats to avoid predatory fish (Resetarits, 1991; Sih et al., 1992). We chose to test the last two behaviors simultaneously because amphibians often re-

spond to predators by changing refuge and habitat use in concert (Resetarits, 1991; Sih et al., 1992).

MATERIALS AND METHODS

Palatability trials.—We tested for palatability of *Dicamptodon* larvae during single encounters with cutthroat trout using paired trials (Formanowicz and Brodie, 1982) in July to September 2001. We used juvenile western red-backed (*Plethodon vehiculum*) and Dunn's (*Plethodon dunni*) salamanders as control prey because they appeared to be fully palatable to cutthroat trout during preliminary trials and they were similar in size to young-of-year *Dicamptodon*. Therefore, we expected that they would serve as a control to demonstrate predation under experimental conditions. We tentatively identified *P. vehiculum* and *P. dunni* to species, and it appeared that 44% were *P. vehiculum*, and 56% were *P. dunni*. However, we could not positively distinguish between the species because of the high proportion of melanistic individuals in this area (Nussbaum et al., 1983) and considered them *Plethodon* spp. The species did not appear to differ in palatability in preliminary trials or a previous experiment (Rundio and Olson, 2001).

For this and following experiments, we collected trout and salamanders from several small streams in the Oregon Coast Range where they coexist (Oak, Parker, Racks, Soap, and Tobe creeks, Benton County, OR). We captured trout (mean fork length [FL] = 179 mm, range = 147–212 mm) by electrofishing and placed them into individual experimental tanks. We fed trout one large earthworm every day at 1600–1800 h for 4–6 days prior to trials to allow them to adjust to experimental conditions and to standardize hunger level. We captured *Dicamptodon* by hand by searching under cover objects in the streams and collected *Plethodon* from stream banks. *Dicamptodon* and *Plethodon* were held for several days prior to trials in separate 40-liter flow-through containers placed in the stream.

We conducted trials in eight 60-liter (54 × 36 × 31 cm) clear plastic tanks placed on the stream bottom in Soap Creek, a 2–4 m wide second-order stream in the MacDonald-Dunn Research Forest of Oregon State University, Benton County, Oregon. Each tank received stream water at a rate of 15–20 liters/min, and water depth was maintained at 25 cm by screened standpipes. We closed the tops of tanks with screen lids, and inserted separate water supply and feeding pipes (50 cm × 2.5 cm diameter

vertical pipes) through the lids. The feeding pipes and small viewing holes in blinds constructed around the tanks allowed us to feed and observe trout without disturbing them.

A trial consisted of offering a trout one *Dicamptodon* and one *Plethodon*, separately, and recording whether each was rejected or consumed. We randomly determined which prey was offered first and offered the second prey to the same trout 24 h later; prey were offered between 1600 and 1800 h. Based on the paired design and to confine the experiment to testing palatability, we analyzed data only from trials in which a trout attacked, and presumably tasted, both prey (Formanowicz and Brodie, 1982). Therefore, if a trout did not attack the first prey we did not offer the second prey and excluded the trial from analysis. We matched *Dicamptodon* and *Plethodon* sizes as closely as possible within a trial, although total lengths of *Plethodon* were slightly larger on average (mean = 64 mm, range = 47–85 mm) than *Dicamptodon* (mean = 61 mm, range = 52–78 mm). We removed salamanders that were not eaten after 0.5 h and tested individual trout and salamanders only once. Based on the paired design, we used McNemar's test (Sokal and Rohlf, 1995) to analyze whether the proportion of trials in which *Dicamptodon* was eaten differed from the proportion in which *Plethodon* was eaten.

In a second experiment, we tested whether *Dicamptodon* palatability varies over repeated offerings to individual trout. We collected five trout (mean FL = 200 mm, range = 190–215 mm) by electrofishing and held them in separate 60-liter flow-through, clear plastic tanks placed in a 0.76 m wide, 5 × 4 m oval indoor stream channel at the Forestry Sciences Laboratory, USDA Forest Service and Oregon State University, Corvallis, Oregon. We filled the channel to 50 cm deep and controlled the water temperature at 12–13 C and current speed at 6–10 cm/sec. Timers on overhead lights maintained a daily photoperiod of 14:10 L:D. We fed trout earthworms for five days to allow them to adjust to the experimental conditions and to standardize hunger level. To minimize disturbance, we fed trout via pipes and observed trials through viewing holes in blinds placed over the clear interior wall of the channel. We offered each trout one *Dicamptodon* larva per day for five days and recorded whether each larva was consumed or rejected. Larvae (mean TL = 58 mm, range = 52–61 mm) were collected several days prior to the experiment and held in a 40-liter flow-through container in a separate channel.

Chemical cue trials.—In this experiment, we tested whether *Dicamptodon* larvae increase refuge use and select shallower microhabitats in response to chemical cues from cutthroat trout. We ran the experiment in eight tank-channel pairs arranged in two rows of four in a shallow riffle in Soap Creek, at the same location as the palatability trials. Stream water was piped at a rate of 15–17 liter/min to each of eight 20-liter plastic tanks (33 × 29 × 22 cm) where we isolated trout. Water depth in tanks was maintained at 16 cm by screened standpipes (2.5 cm diameter), which drained to downstream channels where *Dicamptodon* larvae were held. These channels were 1.35 × 0.48 × 0.25 m plastic livestock feed troughs that drained to the stream via 5.0 cm high standpipes (6.0 cm diameter, screened with 2 × 1 mm mesh). We filled channels with small gravel (6–10 mm diameter) to a depth of 5 cm and inclined them to create a shallow half (0–5 cm deep) at the outlet end and a deep half (5–10 cm) at the inlet end. We placed four unglazed clay tiles (15 × 15 × 0.8 cm) about 15 cm apart down the center of each channel, and elevated one edge of each tile about 2 cm to provide a crevice for refuge. We collected eight benthic invertebrate samples by kick-netting a 1 × 0.35 m area of stream bottom upstream of a 500-μm mesh net, and randomly added one sample to each channel to provide prey for salamanders. Water temperature during the experiment was 12–15 C.

We collected eight cutthroat trout by electrofishing five days prior to the start of the experiment and held them in 60-liter flow-through containers placed in the stream. Trout ranged from 176–213 mm FL (mean = 192) and from 45–99 g (mean = 70). We fed trout earthworms daily but stopped feeding 24 h prior to the experiment. We captured *Dicamptodon* larvae (mean TL = 63 mm, range = 52–77 mm) by hand from streams that contained trout several days prior to the experiment and held them in 40-liter flow-through plastic containers placed in the stream.

We conducted the first set of trials on 20 September 2001. In the morning (1000–1100 h), we stocked the channels with invertebrates, added four *Dicamptodon* larvae to each channel and placed trout in four randomly selected upstream tanks; the remaining four tanks served as controls. That night, we counted the total number of larvae located outside of refuge tiles in each channel at 2200–2230 h using a flashlight with red lens, and also recorded the number in the shallow versus deep halves. (Preliminary trials had revealed that larvae were nocturnal in the experimental channels, and activity peaked about 2 h after dark.) We then removed test animals, scrubbed and rinsed the tanks and channels, and let them flush with stream water for three days before repeating the experiment on 24 September with new animals.

We used permutation tests (Sokal and Rohlf, 1995) to analyze (1) whether the proportion of all larvae that was under refuges was higher in the trout-cue treatments than in controls and (2) whether the proportion of larvae outside refuges that was in the deep end of the channels was lower in treatments than controls. We chose this nonparametric test because of the binomial structure of the data and small sample size.

RESULTS

Palatability.—Palatability during single encounters was assessed from 22 trials in which cutthroat trout attacked both salamander prey. Trout consumed *Dicamptodon* larvae in 95% of trials (21 of 22) and consumed *Plethodon* in all trials. The data did not meet the requirements for McNemar's test because of the complete consumption of *Plethodon*; thus this analysis was not conducted. The single *Dicamptodon* that was rejected died from severe injuries. Twenty-six trials were excluded from analysis because trout did not attack one or both prey, but observations from these excluded trials were consistent with the above results. In 18 of these 26 trials, trout did not attack the first prey offered, and the trial was terminated. Trout attacked, and consumed, a *Dicamptodon* in only one trial. Trout attacked *Plethodon* in seven trials, during which they ate five and rejected two. In the second experiment that tested palatability over repeated offerings, each of five trout consumed all *Dicamptodon* larvae offered.

Chemical cues.—The proportion of all *Dicamptodon* larvae that was under refuge tiles was 60% higher in channels receiving trout cues than in controls (one-sided $P = 0.04$; Fig. 1A). However, the proportion of larvae outside refuge that was in the deep half of channels did not differ between trout-cue and control treatments (one-sided $P = 0.85$; Fig. 1B).

DISCUSSION

In our experiments, young-of-year *Dicamptodon* larvae appeared to have behavioral, but not chemical, defenses against cutthroat trout. Our results from both single and repeated offerings of larvae to trout showed that larvae were palatable and suggest that they are potentially vulnerable to this predator. However, we found
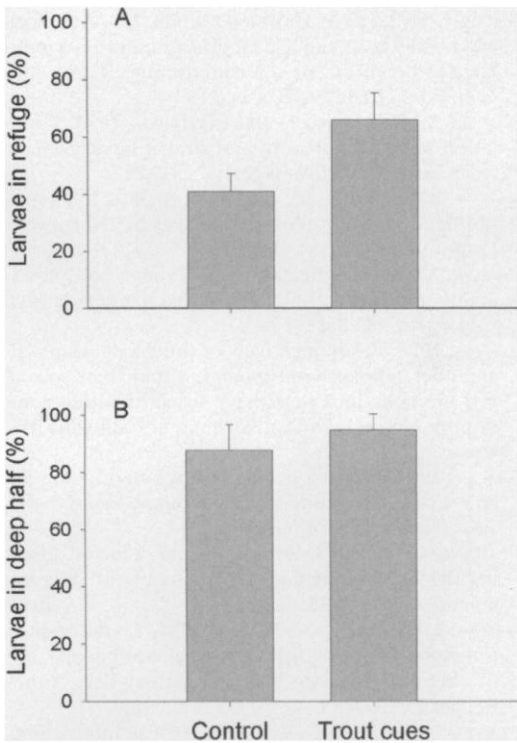
Fig. 1. Proportions (mean ± SE) of *Dicamptodon* larvae in artificial stream pools receiving control water or water with cutthroat trout cues that were (A) under refuge tiles and (B) outside of refuge tiles in the deep half of channels. $n = 8$ for each treatment.

that larvae increased refuge use in response to trout chemical cues, which may reduce the probability of encounters. The ability to detect and react to predator chemical cues is common among palatable amphibians and appears to be important for their coexistence with predators (Kats et al., 1988; Kiesecker et al., 1996; Petranka et al., 1987).

Our results suggest that the availability of refuges may be important for predator avoidance and might influence the distribution and abundance of *Dicamptodon* larvae. This may explain, at least in part, the positive relationship between *Dicamptodon* density and the amount of large, nonembedded stream substrates (Hawkins et al., 1983; Murphy et al., 1981; Wilkins and Peterson, 2000). Rapid (< 2 months) increases in larval density to experimental manipulation of stone density in a northern California stream (Parker, 1991) suggest that this pattern can be produced by behaviors (i.e., microhabitat selection). Changes in population size also may result if survival is higher in habitats with more refuges. Land management activities such as timber harvest and road con-

struction that increase siltation in streams (Waters, 1995) may reduce the availability of refuges to *Dicamptodon* and increase vulnerability to predation.

We did not detect an effect of trout chemical cues on habitat selection by larvae along a gradient of water depth, and larvae were observed almost exclusively in the deepest portion of our channels regardless of treatment. However, our results might not accurately represent this behavior in natural habitats. Because our channels were relatively shallow (0–10 cm), they may have represented habitats in natural streams that generally are free of predatory trout (Bisson et al., 1988). Therefore, larvae may react to trout cues across a more pronounced and natural depth gradient than we presented. Furthermore, habitats in headwaters streams are heterogeneous, and include additional environmental gradients (e.g., substrate and current velocity) and habitat types (e.g., riffles and runs) that may provide *Dicamptodon* larvae with additional choices for habitat selection.

Although we have identified a defense that may contribute to the coexistence of *Dicamptodon* and cutthroat trout in headwater streams, we do not know how this defense affects *Dicamptodon* populations or factors related to fitness. Additional research is needed to estimate the incidence of trout predation on larvae and the effectiveness of refuge use on larval survival. Also, antipredator behaviors often have costs in terms of growth and development (Skelly, 1992; Skelly and Werner, 1990), and experiments are needed to test whether refuge use has sublethal effects on *Dicamptodon*. Finally, more data are needed on the distribution of *Dicamptodon* relative to cutthroat trout to help interpret the importance of this predator-prey interaction compared with other factors (e.g., habitat conditions) potentially affecting *Dicamptodon*.

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