PALATABILITY OF SOUTHERN TORRENT SALAMANDER (*RHYACOTRITON VARIEGATUS*) LARVAE TO PACIFIC GIANT SALAMANDER (*DICAMPTODON TENEBROSUS*) LARVAE.

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Predation can be the principal factor determining the structure and composition of amphibian assemblages (Morin, 1983; Wilbur et al., 1983; Hairston, 1986) and the distribution of amphibian species (Petranka, 1983; Woodward, 1983; Azevedo-Ramos et al., 1999). The impacts of predation, however, can be mediated by antipredator defenses of prey. Differential vulnerability of prey to predators and the patchy distributions of predators often may contribute to variation in the composition and distribution of larval anuran assemblages (Werner and McPeek 1994, Kurzava and Morin, 1998; Azevedo-Ramos and Magnusson, 1999). Unpalatability is a common defense among amphibians (Brodie, 1977) that influences the composition and structure of assemblages (Kurzava and Morin, 1998) and the spatial distribution of prey species (Kats et al., 1988; Azevedo-Ramos and Magnusson, 1999).

In the U.S. Pacific Northwest, giant (*Dicamptodon* spp.) and torrent (*Rhyacotriton* spp.) salamanders occur together in headwater streams but differ in patterns of abundance along longitudinal and microhabitat gradients. *Dicamptodon* is most abundant in perennial streams (Nussbaum and Clothier, 1973; Hunter, 1998; Olson et al., in press), whereas *Rhyacotriton* is most abundant in intermittent or discontinuous headwater streams (Lee, 1997; Hunter, 1998; Olson et al., in press), and occupies shallow microhabitats where it occurs in higher-order streams (Stebbins, 1951; Nussbaum et al., 1983). The causes of this pattern are not known, but the distribution of *Rhyacotriton* may be restricted by physiological limits (Petranka, 1998; i.e., moisture (Ray, 1958) and temperature (Brattstrom, 1963) constraints) or predation by *Dicamptodon* (Stebbins, 1955; Welsh and Lind, 1996). Although *Dicamptodon* is suspected to be the primary predator of *Rhyacotriton* (Nussbaum et al., 1983), predation is known primarily from two

eggs collected from the stomach of a *Dicamptodon* larva in northern California

(Nussbaum, 1969) and from observations of larvae consumed in holding buckets (e.g., in

northern California, R. Bury, pers. comm.). However, *Rhyacotriton* is known to be

noxious to shrews and suspected to be unpalatable to other predators (Nussbaum et al.,

1983). Our objective was to examine predator-prey interactions between Pacific giant (*D.

tenebrosus*) and southern torrent (*R. variegatus*) salamander larvae, and specifically to

assess the palatability of *Rhyacotriton*.

METHODS

We tested the palatability of *R. variegatus* larvae to *D. tenebrosus* larvae in paired

trials after Brodie et al. (1978). We selected *Plethodon dunni* and *P. vehiculum* as control

prey for three reasons: (1) they are potential prey because they occur in and along

headwater streams with *Dicamptodon* and *Rhyacotriton* (Nussbaum et al., 1983; Olson,

unpubl. data); (2) they behaved similarly to *Rhyacotriton* in experimental chambers; and

(3) they were accepted as prey by *Dicamptodon* during preliminary trials, and thus were

likely to function as a control to demonstrate predation under experimental conditions.

We collected animals from intermittent and first-order streams where they co-

occurred on Mary's Peak, Benton County, Oregon. *Dicamptodon* larvae were captured by

electroshocking 48 hours prior to the start of trials and held in pools at the study site in

wire minnow traps (42 cm long by 22 cm diameter, 5.5 mm mesh) with the openings

crimped closed. Larvae ranged from 55 – 82 mm snout-vent length (SVL; $\bar{x}$ = 68) and

109 – 156 mm total length (TL; $\bar{x}$ = 127). Larvae were not fed but were able to feed on

invertebrates that entered the traps. We examined stomach contents from seven larvae

held for 48 hours and found that feeding was reduced compared with uncaged larvae. We assumed that hunger level was similar among larvae by the start of trials.

We captured *Rhyacotriton*, *P. dunni*, and *P. vehiculum* by hand from the stream channel, bank, and splash areas 24 hours prior to the start of trials. To minimize the confounding effect of gape limitation, we collected only individuals less than 50 mm TL. *Rhyacotriton* and *Plethodon* were held in separate flow-through, plastic chambers (45 by 35 by 28 cm, drilled with 2-mm holes) in a pool. Rocks and bark were provided as refugia. We tentatively identified *Plethodon dunni* and *P. vehiculum* to species, and it appeared that 60% were *P. dunni* and 40% were *P. vehiculum*. Due to their small size and the large proportion of melanistic individuals, however, we could not positively distinguish the species from one another and considered them *Plethodon* spp.

Trials were conducted between July 22 and August 13, 1999. A trial consisted of offering a *Dicamptodon* larva one *Rhyacotriton* and one *Plethodon*, separately, for two hours. The order in which prey were offered was assigned randomly, and the second prey was offered 48 hours later. *Dicamptodon* were returned to minnow traps between offerings. *Rhyacotriton* and *Plethodon* were matched in size as closely as possible. When we could not match sizes, we offered slightly larger *Plethodon* ($\bar{x}$ TL = 41.34 mm, range = 33 – 47 mm) than *Rhyacotriton* ($\bar{x}$ TL = 36.26 mm, range = 25 – 47 mm). We conducted ten trials simultaneously, and two sets of trials per day, for a total of 60 trials. Predators and prey were tested only once.

We conducted trials in 15 x 25 x 11-cm clear plastic chambers filled with stream water to a depth of 4 cm. Ten chambers were placed on a platform in the stream such that water about 3 cm deep flowed around the chambers. Chambers were rinsed with stream

water between trials and filled with fresh stream water. Water temperature was 10 – 13 C.

We observed trials for their entirety and recorded the number of attacks on each prey. We defined attacks as contacts between predator and prey in which the prey was bitten by the predator. At the end of each trial, we recorded whether a prey had been consumed or rejected. We examined surviving prey for injuries and examined predator cages for regurgitated prey (predators were held 4 hr from the end of 40 trials and 24 hr from the end of 20 trials). Predators and surviving prey were released to their site of capture.

The independence of the number of prey eaten and prey species was analyzed using Fisher's Exact Test. Only trials in which both prey were attacked were included in analysis.

RESULTS

Dicamptodon attacked both prey in 38 trials. *Rhyacotriton variegatus* larvae survived in 29 of 38 trials (76%) and *Plethodon* juveniles survived 1 trial (3%). Survival was dependent on prey species ($P < 0.0001$, two-tailed test).

The number of attacks preceding consumption or rejection was greater for *Rhyacotriton* than for *Plethodon* ($\chi^2 = 7.26$, df $= 1$, $P < 0.01$). *Dicamptodon* consumed all but three *Plethodon* during the first attack: two were consumed during the second attack, and one was rejected and not attacked again. In contrast, *Rhyacotriton* survived 90% of first attacks: 56% of the consumed *Rhyacotriton* were rejected after the first attack. Of *Rhyacotriton* that survived trials, 28% were attacked and rejected two or more times, to a maximum of seven attacks. Only one of the surviving *Rhyacotriton* showed injuries (a

small laceration to its back). The mean sizes of *Rhyacotriton* consumed and rejected did not differ significantly ($t = 0.50$, df $= 15$, $P = 0.62$, two-tailed test).

Behavior patterns were not quantified but can be summarized qualitatively. Most predators and prey were motionless for the majority of trials but frequently swam or walked the perimeter of chambers for short periods. The majority of encounters resulted in no attack or missed lunges (not included as "attacks" or "rejections"). *Dicamptodon* most often attacked prey that swam near it, although in rare instances *Dicamptodon* stalked and attacked motionless prey. Capture efficiency appeared low and *Dicamptodon* often missed rapidly swimming prey; however, no prey escaped once captured. Most *Rhyacotriton* were either rejected instantly or engulfed into the buccal cavity for several seconds and expelled, but several were expelled after a minute or longer. Most *Dicamptodon* backed away from a *Rhyacotriton* after rejecting it and did not attack it on subsequent encounters.

DISCUSSION

Our results indicate that *Rhyacotriton variegatus* larvae and juvenile *Plethodon* differ in palatability to larval *Dicamptodon tenebrosus*. *Rhyacotriton* was highly unpalatable as evidenced by its survival in most trials. *Plethodon* was readily accepted as prey and survived only one trial. Further, we expect that our results underestimate the effectiveness of unpalatability on the survival of *Rhyacotriton* in nature. Repeat attacks would be less likely in a heterogeneous stream environment that provides escape opportunities.

In contrast to the extensive literature on the palatability of larval anurans and

adult salamanders, we are aware of only two published studies that tested the palatability of larval or juvenile salamanders. Formanowicz and Brodie (1982) showed that *Ambystoma maculatum* and *Notophthalmus viridescens* larvae were palatable to predaceous diving beetles but metamorphic individuals were not. Kats et al. (1988) showed similar results for *A. maculatum*, *A. opacum*, and *A. texanum* larvae to sunfish but found that *N. viridescens* larvae were unpalatable.

The palatabilities of *Rhyacotriton* and *Plethodon dunni* and *P. vehiculum* have been tested in uncontrolled experiments (E. D. Brodie, Jr., pers. comm.). *Rhyacotriton* was noxious to shrews and suspected to be unpalatable to other predators (Nussbaum et al., 1983). *Plethodon dunni* and *P. vehiculum* were unpalatable to birds and mammals (E. D. Brodie, Jr., pers. comm.). Many eastern *Plethodon* are unpalatable to birds and mammals (Dodd et al., 1974; Hensel and Brodie, 1976; Brodie et al., 1979). It is unclear whether our results for *Plethodon* reflect tolerance by *Dicamptodon* or the absence of defenses in juveniles (i.e., there may be an ontogenetic change in palatability; the above studies did not report whether juveniles or adults were tested).

Population differences in palatability and tolerance have been documented in other predator-prey systems. Geographic variation in palatability is known for *Plethodon jordani* (Hensel and Brodie, 1976) and *Taricha granulosa* (Brodie and Brodie, 1990). Brodie and Brodie (1990 and 1991) also found significant variation, both within and between populations, in the resistance of garter snakes (*Thamnophis sirtalis*) to synthetic tetrodotoxin, the neurotoxin found in *Taricha*. Across the ranges of *R. variegatus, Plethodon* spp., and *D. tenebrosus*, populations may have varying degrees of noxiousness or tolerance.

We have challenged assumptions about predator-prey interactions between *Rhyacotriton* and *Dicamptodon* by showing that *Rhyacotriton* survive 90% of encounters with *Dicamptodon*. However, we still do not understand the mechanisms regulating the distributions and abundances of these species well enough to judge the relative importance of physiological constraints and predation. It is likely that both contribute to the distribution of *Rhyacotriton*. Predation by *Dicamptodon* at the level we have measured may be sufficient to result in differential habitat use, and predation by other predators or on other life stages may increase the importance of predation as a primary contributor to assemblage structure.

Kats et al. (1988) and Azevedo-Ramos and Magnusson (1999) showed that unpalatable prey often co-occur with potential predators. Our results are consistent with these studies insofar as *Rhyacotriton* and *Dicamptodon* are sympatric in headwater streams. These studies did not, however, examine the patterns of abundance of unpalatable prey relative to predators. We have found a complementary pattern of abundance of *Rhyacotriton* and *Dicamptodon* at both large (longitudinal stream reach) and small (microhabitat units within reaches) scales (Olson, in press). Our results suggest that although unpalatable prey may persist in habitats with predators, prey may be most abundant in habitats with no or fewer predators. Because patterns of abundance may be more significant ecologically than patterns of presence and absence, we suggest that distributions of unpalatable prey and predators need to be re-evaluated in this context.

ACKNOWLEDGEMENTS

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