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Predation by *Thamnophis couchii* on *Dicamptodon ensatus*

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Recent studies by Gans (1961) and Greene (1983) have discussed the evolution of snakes and indicated, for boids and viperids, an adaptive trend toward feeding on very large prey. In this report we present evidence of this phenomenon in the colubrid genus *Thamnophis.* We have observed *T. couchii* feeding on large larval salamanders: prey ranging up to 88% of snake body weight.

Both *Thamnophis sirtalis* and *T. elegans* are known to eat various species of larval and adult salamanders (Fitch, 1941; Fox, 1952; Gregory, 1978; Kephart, 1982; Lagler and Salyer, 1945). Fitch (1941) found that *T. couchii* occasionally fed on species of newts *(Taricha)* and the Pacific giant salamander, *Dicampfodon ensatus.* Of 325 food items of *T. couchii* examined by Fitch, 4 were species of aquatic salamanders. Fox (1952) also noted that *T. couchii* ate *Taricha* larvae based on laboratory and field observations. To our knowledge, however, there are no reported field observations of *T. couchii* predation on *D. ensatus.*

Field observations of predatory behavior are rare for most reptiles (Greene et al., 1978), including snakes of the widespread genus *Thamnophis.* In the summers of 1986, 1987, and 1988, we made 12 observations of *T. couchii* attacking *Dicamptodon ensatus* at Hurdygurdy Creek (a tributary of the Smith River), in the Del Norte County, California. Four of the observations lasted only a few seconds and ended with the escape of the salamander. This paper reports two of the more lengthy observations, with notes on the others, and includes 24 records of *D. ensatus* from *T. couchii* stomachs.

1.--On the afternoon of 17 July 1986, an adult *T. couchii* was observed attacking a larval, probably neotenic, *D. ensatus,* approximately 0.5 m from the water's edge, on a sandy bank adjacent to a riffle. The snake was approximately 520 mm in total length (TL) and the salamander was approximately 200 mm TL. The snake repeatedly attempted to control the salamander with its body coils and both animals were rapidly biting one another. This activity continued for almost 30 sec until the salamander escaped and swam downstream. The snake raised its head, moved it from side to side, and made apparent visual contact with the salamander, which was resting underwater a few m downstream. The snake entered the water, moved directly toward the salamander, and attacked again. After a few sec of struggling, the salamander escaped and swam upstream, pursued by the snake for approximately 3 m. At this point the snake left the water and the salamander disappeared after swimming further upstream.

2.--Another attack was observed on 11 September 1984 at 1455 h. An adult female *T. couchii,* 554 mm in snout-vent length (SVL), was first observed crawling along the bottom of the creek. After several min of probing in crevices, she darted under a boulder and apparently caught something. However, in the next few sec, a large larval *D. ensatus,* approximately 100 mm SVL, splashed to the surface and swam quickly downstream. The snake appeared to watch it retreat but made no attempt to chase the salamander. When palped, the snake yielded a 40 mm portion of the salamander's tail.

During the course of our study, three other large (>500 mm SVL), adult female snakes were found to have recently ingested portions of larval or neotenic *D. ensatus* tails.

Another noteworthy aspect of several of our observations was how long snakes spent subduing and swallowing prey. Four timed observations of snakes feeding ranged from 3-7 min, with one snake spending over an hour to subdue and swallow an extremely large salamander. The snakes fed on salamanders on shore or in the shallows, swallowing them head first. Most attacks and feeding bouts occurred in the open and, except for the one that spent an hour feeding, the snakes did not immediately seek cover following ingestion.

We analyzed stomach contents of *T. couchii,* from monthly censuses and behavioral observations, at Hurdygurdy Creek during 1986, 1987, and 1988. Of 619 stomachs examined, 215 had contents, and 24 of these were *D. ensatus.* Ten of these observations involved relatively large salamanders (Table 1) and the

TABLE 1. Ingestion and mass ratios for *Thamnophis couchii* feeding on large *Dicampfodon ensatus* at Hurdy-gurdy Creek, Del Norte County, California.

Snake description			Salamander description					
Sex	SVL (mm)	M (g)	Head (mm)	SVL (mm)	M (g)	Diam (mm)	Mass ratio	Ingestion[1] ratio
F	578	92.0	—	133	80.9	32	0.88	—
F	510	51.5	15	92	29.5	22	0.57	1.47
M	446	30.0	10	70	14.0	19	0.46	1.90
F	700	127.8	21	105	56.7	30	0.44	1.43
F	470	47.0	11	82	17.5	19	0.37	1.73
F	550	69.7	16	84	24.8	21	0.35	1.31
F	665	110.0	20	—	34.5	—	0.31	—
F	408	27.3	12	57	7.2	17	0.26	1.42
M	487	43.7	11	66	9.8	15	0.22	1.36
M	292	11.4	8	34	1.6	9	0.14	1.13

[1]Ratio of widest prey diameter to snake head diameter (Greene, 1983). Head diameters were measured by resting the snake's head on a ruler and reading the widest diameter from above. Snakes were only measured in a "relaxed" state, not when exibiting defensive head postures.

others were either small, partly digested, or only a portion of the salamander (e.g., tail only). In the most noteworthy observation the salamander weighed only 12 g less than the snake (Table 1).

Our field observations of snake predation and analysis of stomach contents raise questions relating to foraging behavior and anti-predator tactics. Extensive studies have been conducted under the hypothesis that tail autotomy reduces mortality for many species of lizards and salamanders (Wake and Dresner, 1967; Congdon et. al., 1974; Maiorana, 1977; Vitt et al., 1977; Arnold, 1982; Vitt, 1983). Our observations of tail loss by *D. ensatus* confirm the value of this mechanism as an anti-predator tactic for this species. The long and easily broken tail of larval and neotenic *D. ensatus* provides a method of escape from aquatic predators. Unfortunately, little is known about the frequency of use and physiological implications of this anti-predator tactic.

Several investigators have discussed the development of feeding mechanisms and foraging behavior and their significance in snake evolution (Gans, 1961; Greene and Burghardt, 1978; and Greene, 1983). Greene (1983) presented a scenario for early snake evolution based on diet and, specifically, prey size and shape. He suggested that morphological changes in jaw structure allowed early snakes to take a greater variety of prey. For boids (the second major radiation) and viperids (an element of the third major radiation), this ability led to the behavior of feeding infrequently on large prey versus feeding frequently on small prey. Modern snakes, other than viperids, have not necessarily followed this trend, and instead display a wide variety of foraging behaviors (Greene, 1983).

Our observations indicate that adult *T. couchii* can feed on large prey, in this case, large larval or neotenic *D. ensatus.* The ingestion and mass ratios calculated for our observations indicate that these snakes are able to take prey that approach their own body weight and that have body diameters that greatly exceed the head diameter of the snake (Table 1).

There are various costs and benefits of feeding infrequently on large prey. Among the costs are increased time and energy spent subduing and swallowing prey, and reduction of mobility after ingestion of a large meal; both resulting in increased vulnerability to predators. Garland and Arnold (1983) found that endurance distance and time were significantly lower for juvenile *T. elegans* that had fed recently. These snakes were force-fed meals ranging from 18-27% of their body weights, relatively low values compared to our observations. In situations where the weight of the prey approaches the snake's body weight, it is likely that mobility would be greatly reduced thus increasing vulnerability to predators. However, feeding infrequently may result in less exposure to predators overall. Pough and Andrews (1985) concluded that energy maximization per unit time may not be biologically important for most lizards; rather, they speculated that minimization of exposure to predators, via feeding infrequently, would ultimately explain the apparent affinity many lizards have for large prey. Further studies of food habits along with field observations of predatory events would provide valuable information on these aspects of snake diet and their evolutionary implications (see Voris and Moffett, 1981).

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