Ontogenetic Changes in the Foraging Behavior, Habitat Use and Food Habits of the Western Aquatic Garter Snake, *Thamnophis couchii*, at Hurdygurdy Creek, Del Norte County, California

by

Amy J. Lind

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by

Amy J. Lind

Approved by the Master's Thesis Committee

David W. Kitchen Nov 15, 1990
David W. Kitchen, Chairman Date

Nov 15, 1990
Gerald M. Allen Date

Nov. 15, 1990
C.J. Ralph Date

Nov 13, 1990
Hartwell Welsh Date

Nov 19 '90
Director, Natural Resources Graduate Program Date

90/W-203/11/12
Natural Resources Graduate Program Number

Approved by the Dean of Graduate Studies

Susan H Bicknell 1/27/91
Susan H. Bicknell Date

ABSTRACT

I studied the foraging behaviors, stream habitat use, and food habits of a marked population of western aquatic garter snakes, *Thamnophis couchii*, at Hurdygurdy Creek (Del Norte County, California) during the spring and summer of 1987 and 1988. Data were collected using a portable computer with a running clock so that a continuous record of behaviors and habitat use was obtained for each snake observed. Snakes were placed into three age/size classes, (neonate, juvenile, and adult) and all analyses were done among these classes. Adults foraged more actively and in a wider variety of stream habitats than either juveniles or neonates. Adults also fed on a wider variety of prey types and sizes, especially concentrating on large, stream substrate-dwelling Pacific giant salamander (*Dicamptodon ensatus*) larvae and neotenes. Juvenile and neonate snakes fed on prey that primarily inhabited shallow stream margins. Consumption of relatively large prey by adults and smaller prey by juveniles indicated a shift in foraging modes; from frequent feeding on small prey to infrequent feeding on large prey. These ontogenetic changes in foraging behavior, habitat use and food habits of western aquatic garter snakes are probably the result of a combination of ecological, morphological, and physiological constraints and suggest partitioning of prey and habitat.

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INTRODUCTION

Few observers have attempted to quantify the foraging behaviors of snakes (Drummond, 1983). Some information is available on snakes of the largest family, Colubridae (Arnold, 1980; Drummond, 1983; Gillingham, 1986) and also the family Viperidae (Reinert et.al., 1984; Duvall et.al., 1985). In addition, there is little information about ontogenetic changes in snake foraging behavior and foraging modes (e.g., "sit-and-wait" and active; Schoener, 1971)(Burghardt, 1978; Mushinsky, 1987).

Food habits studies of several species of water snakes (Colubridae: *Nerodia* spp.) and sea snakes (Hydrophididae) indicated that both size and type of prey changed as snakes matured (Voris and Moffet, 1981; Mushinsky et al., 1982; Plummer and Goy, 1984). In the case of water snakes, prey size increased with snake size, while sea snakes took a wider range of prey sizes as they matured, but did not forage exclusively on larger prey. These studies indicate differential foraging among juvenile and adult snakes, but documentation of the ecological constraints governing the use of different behaviors and foraging modes is limited (Huey and Pianka, 1981; Mushinsky, 1987). Ecological factors such as habitat structure, ambient temperatures, prey availability, exposure to predation, and resource partitioning should be considered along with physiological and morphological limitations on foraging for different sized snakes (Mushinsky, 1987).

The Colubrid genus *Thamnophis* is widely distributed in North America and contains several species that are among the most abundant of all snakes (Stebbins,1985; Conant,1958). Most species in the genus are diurnal and many forage in open habitat, presenting a unique opportunity for field observations of foraging behavior.

The western aquatic garter snake (Thamnophis couchii) is primarily aquatic in its habits, foraging in and along streams (Fitch, 1941; Stebbins, 1985). The aquatic nature of this species adds another dimension to the ecological and physiological factors influencing behavior. The thermal gradient experienced while moving between land and water undoubtedly affects both the mobility and metabolism of these ectotherms (Stevenson et al., 1985) and some compensating mechanism (behavioral or physiological) probably exists that allows maintainence of preferred body temperatures (Burkett, 1966; Fleharty, 1967; Osgood, 1970). Foraging in water also requires a mechanism to control buoancy and breathing rate, in order to maximize efficiency.

My objectives were to quantitatively describe and compare the foraging behaviors, stream habitat use, and food habitats of three age (size) classes of western aquatic garter snakes: neonates, juveniles, and adults. I addressed the following questions: (1) Does the use of foraging behaviors and foraging mode vary among snake age classes ? (2) does stream habitat use vary among age classes ? and (3) do food habits differ among snake age classes ? Information on attack behaviors and foraging success also was gathered.

STUDY AREA

All field work was done on the lower five kilometers of Hurdygurdy Creek in Del Norte County, California (Fig. 1) at an altitude of 200-250 meters. Hurdygurdy Creek is a tributary of the south fork of the Smith River and is located on the Gasquet District of the Six Rivers National Forest. The stream ranges from 10 to 15 m wide and has mainly cobble and boulder substrate. There is a fairly narrow, though quite variable, zone (5-25 m) of riparian vegetation consisting of alders (Alnus spp.), willows (Salix spp.), and big leaf maple (Acer macrophyllum). Upland vegetation is Douglas-fir (Pseudotsuga menziesii) with California laurel (Umbellularia californica), incense-cedar (Calocedrus decurrens), huckleberry (Vaccinium spp.), California hazel (Corylus cornuta), and poisonoak (Toxicodendron diversiloba). A variety of wildlife species and sign were seen in and along the creek during the course of the study (Table 1).

The climate is temperate; summer highs ranged from 25-35 ^{o}C and lows from 8-13 ^{o}C. Winter rainfall is heavy, especially at higher elevations, and averages 280 cm (range 152-330 cm) (M. Furniss, pers. comm., USDA Forest Service, Six Rivers National Forest, 501 5th Street, Eureka, CA 95501). Historical land use in the Hurdygurdy Basin has been mainly logging (by the Gasquet District of Six Rivers National Forest) and mining by a variety of small private operators (Syda, 1990). The geology of Hurdygurdy Basin is a Jurassic ophiolite series of metamorphosed sedimentary and volcanic rock. Most bedrock has been strongly folded and sheared and the significant variation in erodibility of formations has led to a melange of stable and unstable

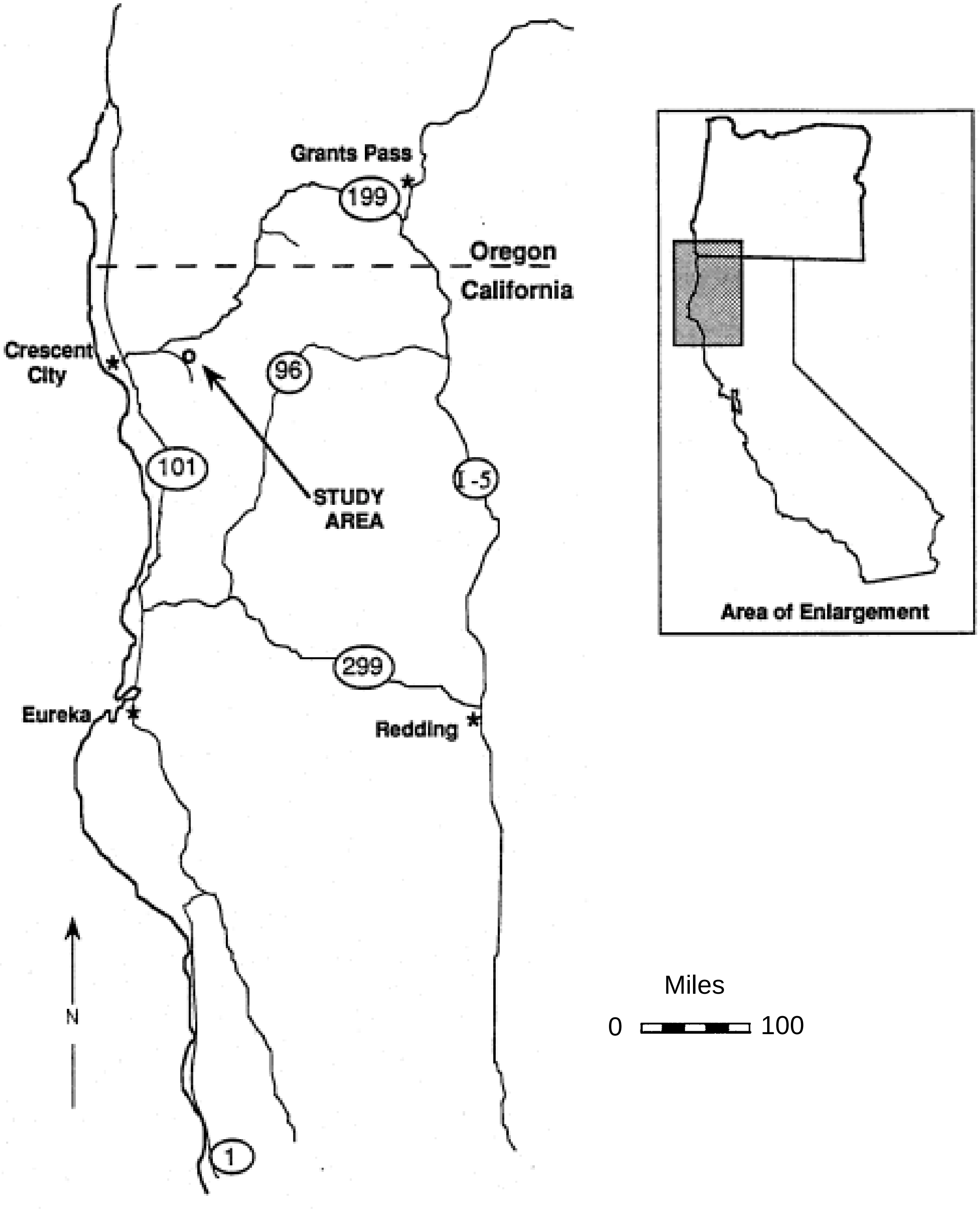

Figure 1. Location of Hurdygurdy Creek Study Area in Northern California.

Table 1. Vertebrate Wildlife Species Observed Along Hurdygurdy Creek (Del Norte County, California) During 1987 and 1988 Field Work. Potential Ecological Relationships to Western Aquatic Garter Snakes are Indicated.

Common Name	Scientific Name	Ecological Relationships
Steelhead trout	*Oncorhynchus mykiss*	prey, competitor
Pacific giant salamander (larvae and neotenes)	*Dicamptodon ensatus*	prey, competitor
Foothill yellow-legged frog	*Rana boylei*	prey
Northwestern garter snake	*Thamnophis ordinoides*	competitor
River otter	*Lutra canadensis*	predator, competitor
Great blue heron	*Ardea herodias*	predator, competitor
American common merganser	*Mergus merganser*	competitor
Western red-tailed hawk	*Buteo jamaicensis*	predator
American osprey	*Pandion haliaetus*	predator, competitor
Spotted sandpiper	*Actitus macularia*	competitor
Steller's jay	*Cyanocitta stelleri*	predator
Western belted kingfisher	*Megaceryle alcyon*	competitor
North American Dipper	*Cinclus mexicanus*	competitor

areas (T. Lisle, pers. comm., USDA Forest Service, Pacific Southwest Forest and Range Experiment Station, Redwood Sciences Lab, 1700 Bayview Drive, Arcata, CA 95521). For more information on the geology of the Smith River area see Harper (1980).

METHODS

Background

An autecological study, investigating food habits, habitat associations, and demographics of the Hurdygurdy Creek population of Western aquatic garter snakes, was started in the summer of 1986 by the Timber/Wildlife Habitat Relationships Unit at the Redwood Sciences Laboratory, USDA Forest Service, Pacific Southwest Forest and Range Experiment Station (Welsh, 1987). This study was complimentary to a basin-wide study on anadromous fish habitat use and distribution (Decker and Lisle, 1985). The autecological study of garter snakes included monthly censuses (May through September) of an approximately 5 km section of the stream and provided a marked population of snakes. The term "census" will be used for all further references to this study. I used data from the census study to develop relationships between snake body size and age class for my behavioral study. The census study also provided background information on activity periods and stream habitat associations of the snakes. Food habits data from the censuses were used as I felt this data was less biased than similar data collected during behavioral observations.

Behavioral Observations

The two most common methods used to gather data for activity budgets and to quantify behavior, are instantaneous sampling and continuous observation (Altmann, 1974). In instantaneous sampling, the activity of an animal is recorded at the end of a timed interval. In continuous observation, activities are continually recorded and timed. The weakness of the instantaneous sampling method is that it gives no information on the durations of activities (Partridge 1976). Both instantaneous sampling and continuous observation were used by Drummond (1983) in his study of water and garter snake foraging behaviors. My study of Thamnophis couchii relied primarily on the continuous observation method as employed by Drummond.

I observed snakes from May through September in both 1987 and 1988, between 0900 and 1800 hours, the primary period of activity. A portable data collector (PDC), OmniData Polycorder 601, was used to make observations of snakes along the stream (Hensler et al., 1986). The PDC has a built-in clock and was programmed to record changes and durations of different behaviors and stream habitat use (Table 2), providing a continuous account of individual activities. Individual snakes were observed for as long as possible. However, two minutes was the minimum observation length used for analysis.

Behaviors were defined with an emphasis on foraging behavior and included: "peering", "craning", "underwater substrate-crawling", and "margin-wandering" (after Drummond, 1983) (Fig. 2). Drummond's "cruising" behavior was modified for this study. I used it to describe snakes that were actually moving across the water surface (Fig. 2), whereas Drummond used it to for snakes that were either moving on the water, or resting on shore and moving just their head and neck on the surface of the water. Two additional categories, "basking/ resting" and "ambush position" (Fig. 2), were included as none of Drummond's behaviors appeared to be appropriate. I also ommitted several

Table 2. Descriptions of Stream Habitat Types at Hurdygurdy Creek, Del Norte County, California (Modified from Bisson et al., 1981 and McCain et al., 1990).

Low Gradient Riffles were relatively shallow areas (10-50 cm)[a] with turbulent water and exposed substrate. Gradient was ≤ 4% and substrate was mostly pebble and cobble[b].

High Gradient Riffles were areas that were relatively deep (10-50 cm) with swift flows, very turbulent water and large amounts of exposed substrate. Gradient was >4% and substrate wa mainly boulder.

Runs were moderately deep areas (20-100 cm) with swift flows, but few flow obstructions, and little to no turbulence. Substrates were usually gravel, pebble, cobble, boulder.

Glides were wide, relatively shallow areas (30-90 cm), with low to moderate flow rate and no surface turbulence. Substrate was usually sand, gravel, pebble, and cobble.

Mid-Channel Pools[c] were large, relatively deep (90-240 cm) pools formed by mid-channel scour. Water velocity was slow, with variable substrates.

Edgewaters were relativley shallow areas (10-40 cm) with little or no flow, in stream margins. They were often found associated with main channel riffle habitat, but small amounts occurred along nearly all main channel stream habitats. Substrate was mainly pebble, cobble, and boulder.

On Shore. This habitat category was used for snakes that were moving along the stream bank and obviously not using or oriented toward a particular stream habitat.

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[a] Depth ranges are from Decker and Lisle (1985; unpublished data).

[b] Substrate size class diameters in mm (Lane, 1947):

sand	.0625	-	1.0
gravel	1.0	-	32.0
pebble	32.0	-	64.0
cobble	64.0	-	256.0
boulder		>	256.0

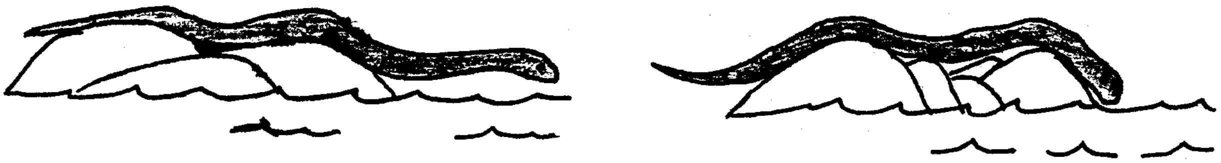
[c] All pools, other than edgewaters were categorized as MCP's, because snakes rarely used these habitats. A more refined system is available in Bisson, et al. (1981) and McCain, et al. (1990).

INACTIVE NON-FORAGING BEHAVIORS

Basking/Resting - lying mostly out of the water; head is not oriented toward the water.

Peering - head is well above water, but oriented toward it.

SIT AND WAIT FORAGING BEHAVIORS

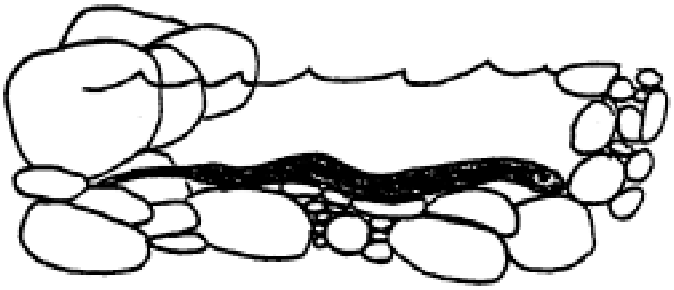


Craning - body out of water, head extended out over water, looking and tongue-flicking at prey.

Ambush Position - body out of water, head oriented toward water and within a few cm of it; looking and tongue-flicking.

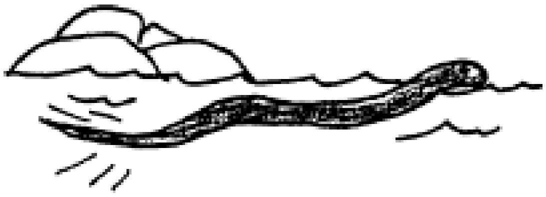
Figure 2. Behaviors of Western Aquatic Garter Snakes at Hurdygurdy Creek (Del Norte County, California) 1987 and 1988. Behaviors Are Modified from Drummond (1983); General Behavioral Modes (e.g. "Active Foraging") Are My Categories.

ACTIVE FORAGING BEHAVIOR



Underwater Substrate-Crawling - completely submerged, crawling along stream bottom, probing in crevices and tongue-flicking.

ACTIVE NON-FORAGING BEHAVIORS



Cruising - body in water, floating on surface, head out of water, used to get from place to place.

Margin-wandering - body is out of water, on shore, crawling on substrate to get from place to place.

Figure 2. Behaviors of Western Aquatic Garter Snakes at Hurdygurdy Creek (Del Norte County, California) 1987 and 1988. Behaviors Are Modified from Drummond (1983); General Behavioral Modes (e.g. "Active Foraging") Are My Categories. (continued)

behaviors of Drummond's: "underwater open-mouth search", and several types of dives, as they were rarely seen in my population. I categorized behaviors into four general types: inactive non-foraging (basking/resting and peering); sit-and-wait foraging (craning and ambush position); active foraging (underwater substrate-crawling); and active non-foraging (cruising and margin-wandering) (Fig. 2). Attacks on various prey and outcome of the attack (i.e., successful capture of prey or failure to capture prey) were included as part of each sequential observation.

The distance at which observations were made varied depending on the activity of the snake when it was first located. Snakes that were underwater or appeared occupied with an activity were observed from short distances (1-5 m) since they were not easily disturbed. Snakes that were inactive were observed from longer distances (10-20 m), with binoculars if necessary, to prevent disturbance. It was obvious when a snake became aware of an observer: it oriented toward the observer, moved its head quickly from side to side, and tongue-flicked. At the first sign of escape behavior, observations were terminated. At the end of each observation period the snake was captured, if possible, and the following data were collected: date, sir and water temperature (^{o}C) (proximal to the snake), cloud cover, sex (Fitch, 1987), snout-vent and total length (mm), weight (gm), head diameter, at widest point(mm), distance moved during the observation (ocularly estimated, in decimeters), water depth, for snakes in or oriented toward the water (five depth classes: <1 - 10 cm, 11-20 cm, 21-30 cm, 31-40 cm, 41-50 cm), location (based on habitat maps from Decker and Lisle, 1985), and stomach contents collected by palping. Snakes were palpated gently from vent to mouth to force regurgitation of recently ingested prey items (Fitch, 1987).

All unmarked snakes were given unique numbers when captured (Ferner, 1979; Fitch, 1987). The marking technique differed from that used for censuses being conducted in the area. The starting point for snakes marked during behavioral observations was in the middle of the snake's body and was designated by a clipped ventral scale. The first scale above the start point was scale one, followed by scale two, etc. Snakes marked in this way were recorded as being in the 1000 series (i.e., the first snake marked was 1001) so that behavioral observations could be sorted from census observations. For snakes that escaped capture (14.3% of observations), I estimated age/size class, but all other body measurements and stomach contents were ommitted.

Data Analysis

Data from three years of monthly censuses (Welsh, 1987) were used to determine age/size classes for this study. Snakes were considerd neonates from parturition (usually in August or September) until they sought winter cover (probably in late October, depending on the weather). Juveniles included snakes that emerged from their first winter to those with a snout-vent length (SVL) of 449 mm. Adults were 450 mm SVL or larger. The final designation of adults as 450 mm SVL or greater, was based on three factors: (1) the size of the smallest gravid female snake (455 mm SVL), (2) growth rates and natural size (year) class breaks in the census data, and (3) evidence of size at maturity for other species of Thamnophis (White and Kolb, 1974; Garcia and Drummond, 1988). At 450 mm SVL, adults were probably 2 1/2 - 3 years old. This size class break was used for both males and females, though males probably mature at a smaller size. A field technique to collect sperm is required to determine maturity (Fitch, 1987) and sperm were not collected during the census study (Welsh, 1987). Therefore, no clear determination of sexual maturity could be made for males. The term age class will be used from here on to refer to these three ages/sizes of snakes.

Several procedures were followed to assure independence of behavioral observations: (1) snakes were individually marked, (2) observations were made throughout the census study area (e.g., no areas were sampled exclusive of others), and more importantly, (3) the individual was the unit of analysis. That is, each sequential observation of an individual was considered to be a single observation only. Lengthy observations were not broken into smaller segments to increase sample size.

Of all captured and marked snakes (n = 132), only six were observed twice, and in each case these observations were at least one month apart. Snakes that escaped capture, made up only 14.3% of all observations.

I tested (Chi-square contingency table analysis) for year to year differences in behavior and habitat use for each age class. Only adults showed a significant difference in behaviors for all categories. I attributed this difference to the low sample size of adults in 1987 and to my improved ability to find undisturbed adults foraging in 1988. Adults did not show a significant difference between years for foraging modes or habitat use, so for all analyses of behavior and habitat use, I combined data from 1987 and 1988 to improve overall sample sizes. I also tested (Chi-square contingency table analysis) for effects of sex on behavior for each age class and found none. Therefore, I combined observations of males and females in all analyses.

Simple linear regression was used to relate rate of movement to size of snakes. Estimated distances were corrected for the length (in minutes) of the observation, resulting in a rate (meters per minute) that I used for comparisons across the range of snake snout-vent lengths.

Each behavioral observation was treated two ways. First, one behavior and its associated habitat were chosen systematically from the sequence of behaviors for use in contingency table analyses. I chose the behavior and associated habitat that occurred at the mid-point of the observation (i.e., if the observation was 12.8 minutes long, the behavior and habitat at 6.4 minutes represented that observation). Secondly, each observation (all behaviors in the sequence) was placed in one of three categories that described the general foraging mode: sit-and-wait; active; or a combination (Fig. 2). If only sit-and-wait foraging behaviors were observed, then the observation was categorized as sit-and-wait. If only active foraging behaviors were observed, then the observation was categorized as active, and if both types of behaviors were observed, then the observation was categorized as a combination. If no foraging behaviors were observed (23 observations; 15%) then that observation was omitted from analysis of foraging mode.

However, all observations were included in analyses of habitat and water depth use. I felt it was important to examine habitat associations for all activities even if I saw no specific foraging behaviors during an observation.

Chi-square tests for association (independence) were used to evaluate the relationship between snake age class and the following variables: behavior (systematically chosen), foraging mode, stream habitat use, water depth, and a variable representing habitat and water depth. The latter variable combined habitats into two categories: slow moving (glides, mid-channel pools, and edgewaters); fast moving (low and high gradient riffles and runs), and water depth into two categories: shallow (<1-10 cm); and deep (> 10 cm). All possible combinations of these categories were examined: slow and shallow; slow and deep; fast and shallow; fast and deep. This combination variable provided a way to analyze two related physical aspects of the stream habitat as one variable; a habitat/water depth index.

There is concern among some statisticians that contingency tables with more than 20% of expected values equaling five or less, may provide biased results (Zar, 1984:70). The combination variables, foraging mode and the habitat/water depth index, were used to reduce the number of cells in the contingency tables. For all contingency table analyses the $p \leq 0.05$ significance level was used to indicate a relationship of dependence between snake age and the variable of interest (Zar, 1984:61).

Food habits data from 1987 and 1988 censuses (H. Welsh, unpublished data, USDA Forest Service, Redwood Sciences Lab, 170

Bayview Drive, Arcata, CA 95521) were tested (Chi-square contingency table analyses) for differences among snake age classes. Only snakes with stomach contents were included. Food habits from behavioral observations were not used as I felt the sample was not as valid as census observations. Several aspects of behavioral observations could have introduced biases in food habits data. Observations were made only on undisturbed snakes (i.e., snakes that were alerted to the observer were passed by), snakes were watched for various lengths of time, and some observations included feeding episodes, while others did not. In censusing, all snakes seen were captured, providing an unbiased and random sample of food habits. Mobility and endurance are often reduced after eating (Garland and Arnold, 1983) and full snakes are probably more weary than empty snakes. It is likely that most snakes included in behavioral observations had empty stomachs, whereas snakes captured in censuses could have been full or empty.

Observations of prey attacks are described and presented graphically due to small sample sizes among age classes. Attack success rate was defined as the proportion of individuals in an age class that were observed to attack and successfully capture a prey item. It does not reflect multiple observations of one individual.

RESULTS

Seasonal Distribution of Behavioral Observations

During the spring through late summer of 1987 and 1988, 154 behavioral observations of three age classes of *T. couchii* were made (Table 3). The total actual observation time was 32.4 hrs. Average durations of observations differed slightly between age classes. Observations were made throughout the primary annual activity period of snakes (May through September), though weather and logistical constraints prevented equal sampling in each month and year (Fig. 3).

Foraging Behavior and Stream Habitat Use

Regression analysis of distance moved (meters/min) versus snake snout-vent length indicated that larger snakes moved faster than smaller snakes (Fig. 4). Mean rate of movement by age classes were: neonates - 0.08 m/min (s.d. ± 0.09); juveniles - 0.22 m/min (± 0.24); and adults - 0.44 m/min (± 0.73).

Frequency of use of behaviors and foraging modes was significantly associated with age (Table 4). However, in the analysis of all behaviors, half the contingency table cells had expected values less than five; these cells contributed little to the overall chi-square value (Appendix A). Neonates generally used sit-and-wait behaviors, adults used mainly active behaviors, and juveniles used combinations of both (Figs. 5 and 6). The primary differences were in the use of ambush and underwater substrate-crawling behaviors.

Table 3. Summary of Behavioral Observations of Western Aquatic Garter Snakes (Thamnophis couchii) by Age Class at Hurdygurdy Creek (Del Norte County, California) in 1987 and 1988.

Age Class	Sex[a] n	F	M	U	SVL (mm)[b,c]	Mass (g)[c]	Duration of Obs.(min)[c]
Neonates	28	17	9	2	196.3 (179-226)	3.3 (1.7-5.00)	14.25 (4.50-37.20)
Juveniles	81	41	32	8	341.9 (188-446)	16.9 (3.5-44.0)	12.97 (1.97-46.17)
Adults	45	16	17	12	537.6 (451-700)	65.1 (30.0-184.0)	11.06 (1.47-82.00)
All	154	74	58	22	362.2 (179-700)	25.6 (1.7-184.0)	12.6 (1.47-82.00)

[a] sex: F = female, M = male, U = unknown (escaped snakes)

[b] SVL is snout to vent length

[c] mean and (range)

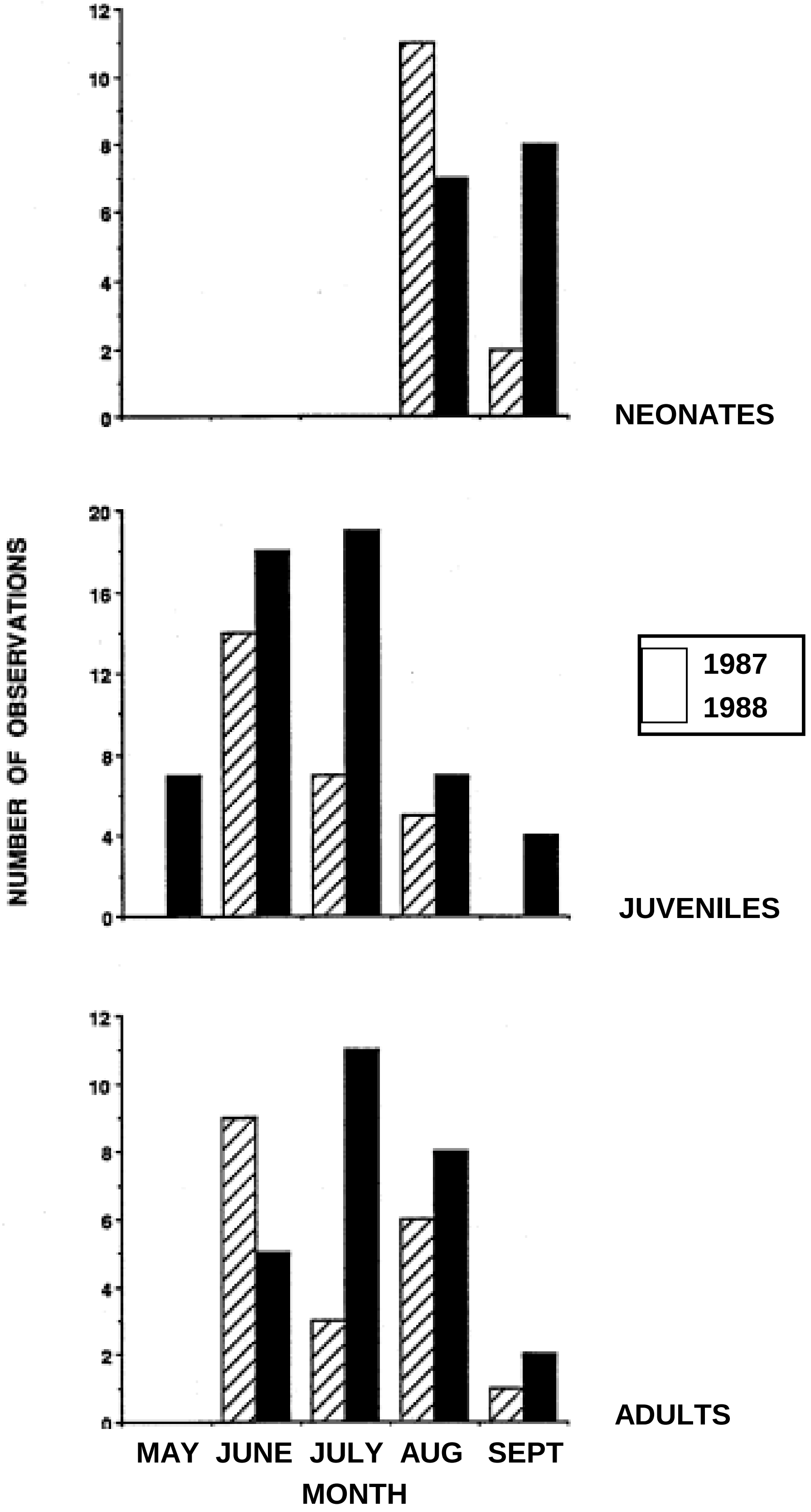


Figure 3. Numbers of Observations of Western Aquatic Garter Snakes by Month/Year.

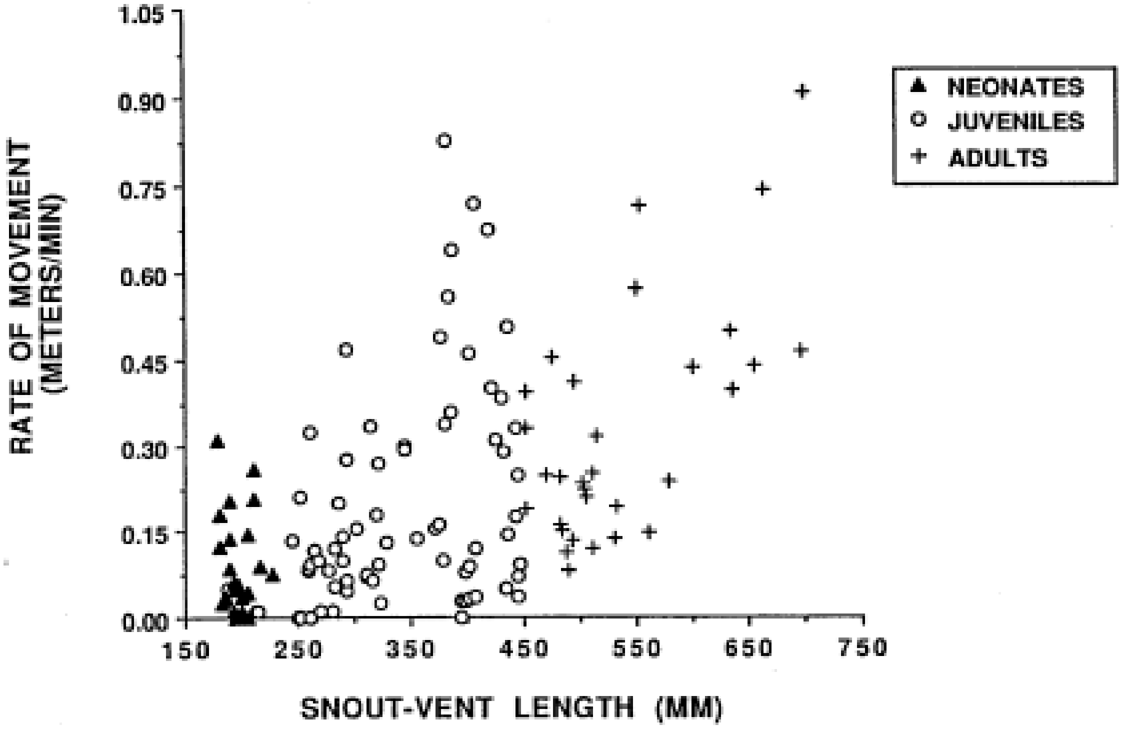


Figure 4. The Relationship Between Rate of Movement and Size of Snakes by Age Class; r-sqr (adj) = .313, F - 59.67, p = <0.0001.

Table 4. Chi-square Contingency Table and P Values for Comparisons of Association of Western Aquatic Garter Snake (*Thamnophis couchii*) Age Class with Behavior, Stream Habitat and Water Depth Use, and Food Habits at Hurdygurdy Creek (Del Norte County, California) in 1987 and 1988.

Age Class vs:	Chi-square value	p-value	Degrees of Freedom
Behavior (8 types)	42.45	0.0001	14
Foraging mode	63.23	<0.0001	4
Habitat	56.02	<0.0001	12
Combined habitat (slow and fast)	28.77	<0.0001	2
Water depth (5 depth classes)	46.76	<0.0001	10
Combined water depth (shallow and deep)	40.91	<0.0001	2
Combined habitat and water depth index	54.65	<0.0001	6
Food habits from census study	27.68	<0.0001	4

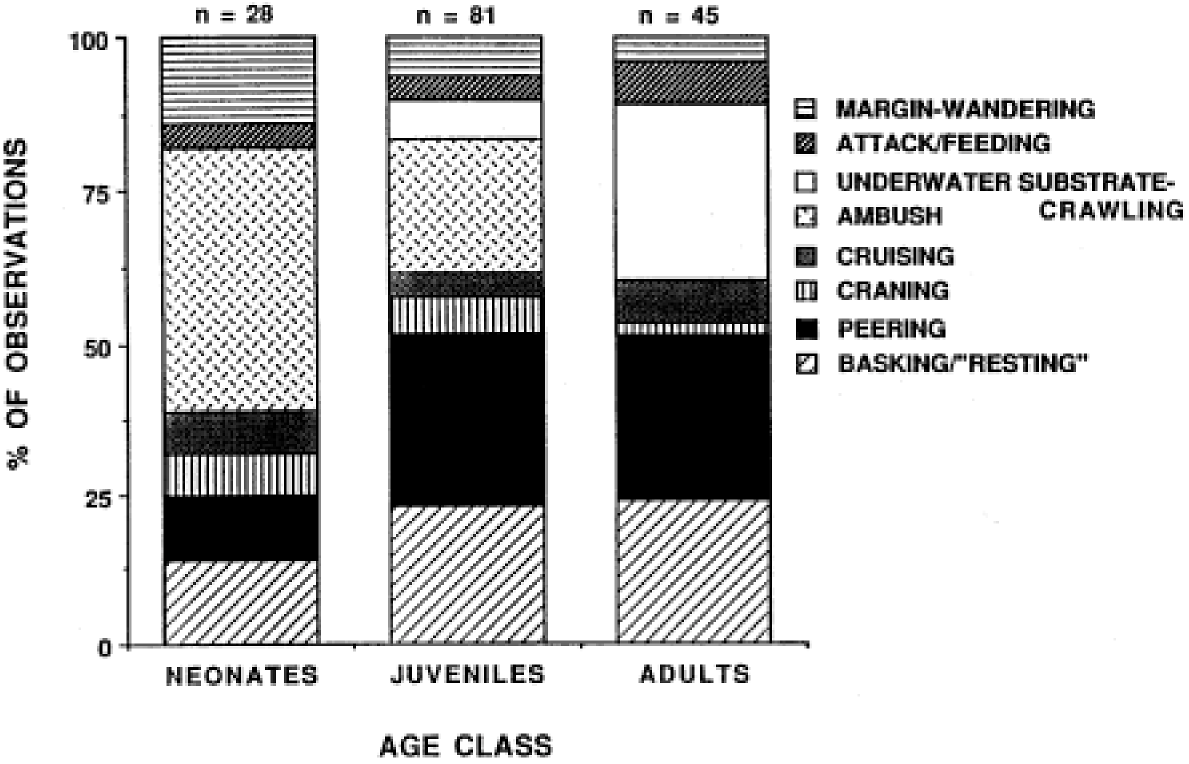


Figure 5. Use of Behaviors by Three Age Classes of Snakes; Chi-sq = 42.45, p = 0.0001, n = Total Number of Individuals Observed in Any Age Class.

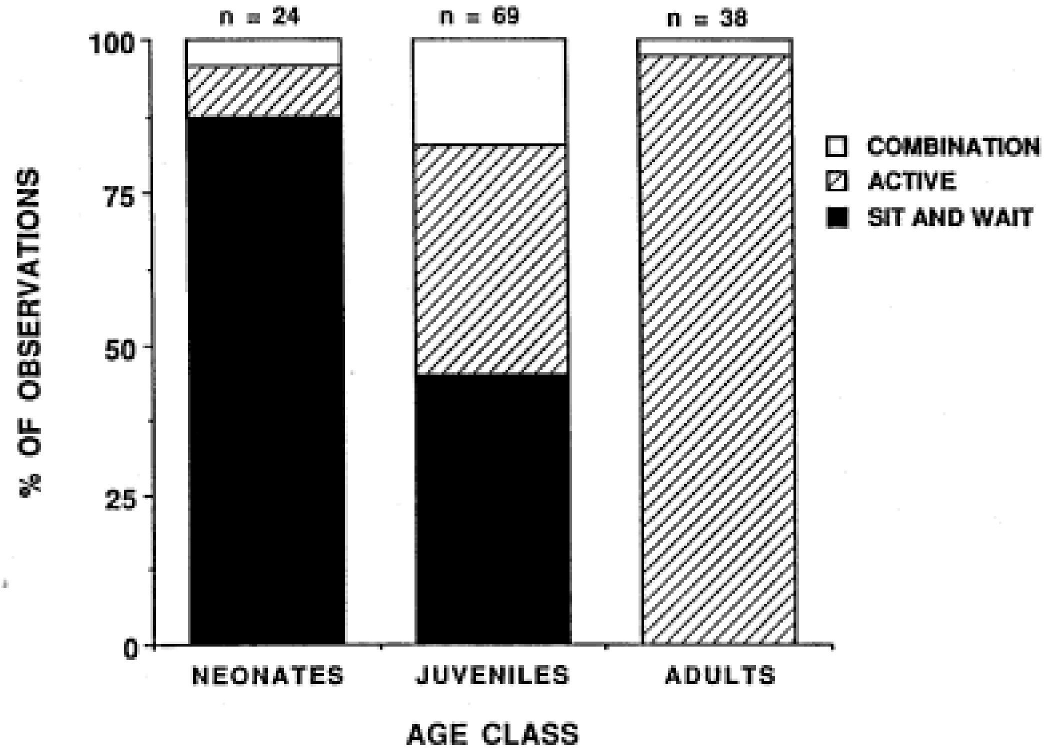


Figure 6. Use of Foraging Modes by Three Age Classes of Snakes; Chi-sq = 63.23, p <0.0001, n = Total Number of Individuals Observed in Any Age Class.

Neonates most often used an ambush position for foraging. Juveniles used both ambush and underwater substrate-crawling behaviors. Adults used underwater substrate-crawling almost exclusively (Fig. 5 and 6). Other non-foraging behaviors such as basking and margin-wandering appeared to be used equally among age classes (Fig. 5).

Stream habitat and water depth use also were significantly associated with age class (Table 4). As with behavior, a large proportion of both habitat and water depth contingency table cells had expected values less than five (Appendix A). These cells account for almost half of the overall chi-square value, though the value is so large it would be significant without them. Adults used a wider variety of habitats and water depths than did neonates or juveniles (Figs. 7 and 8). Neonates appeared to be the most specialized; over 80% were found foraging in shallow (<10 cm) edgewaters. Adults foraged mainly in fast-moving water with depths up to 0.5 m, and juveniles foraged in relatively shallow riffles and edgewaters (Figs. 7 and 8).

The combined habitat and water depth categories were significantly associated with age class (Table 4). The most striking differences were between neonates and adults, with juveniles falling somewhere in between (Fig. 9).

Food Habits

Of 294 snakes captured during 1987 and 1988 censuses, 86 (29.3%) had stomach contents. The proportion of full stomachs differed among

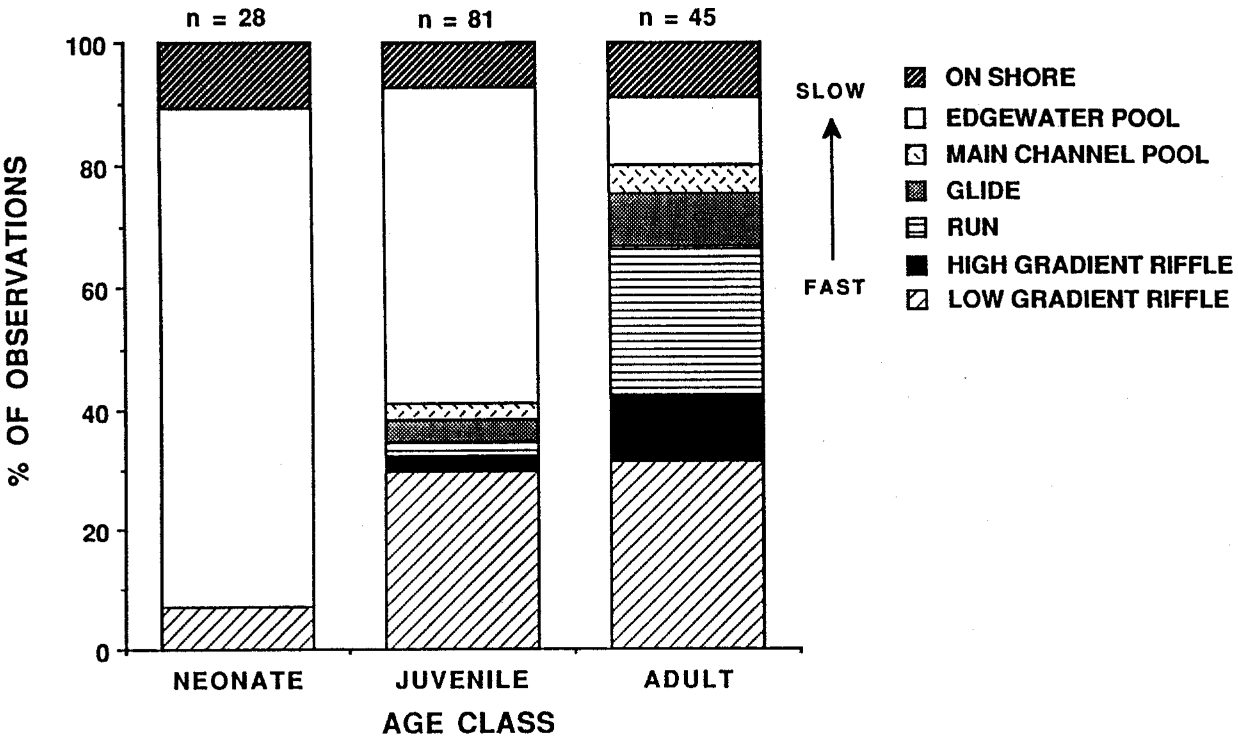


Figure 7. Use of Stream Habitats by Three Age Classes of Snakes; Chi-sq = 56.02, p <0.0001, n = Total Number of Indivduals Observed in Any Age Class.

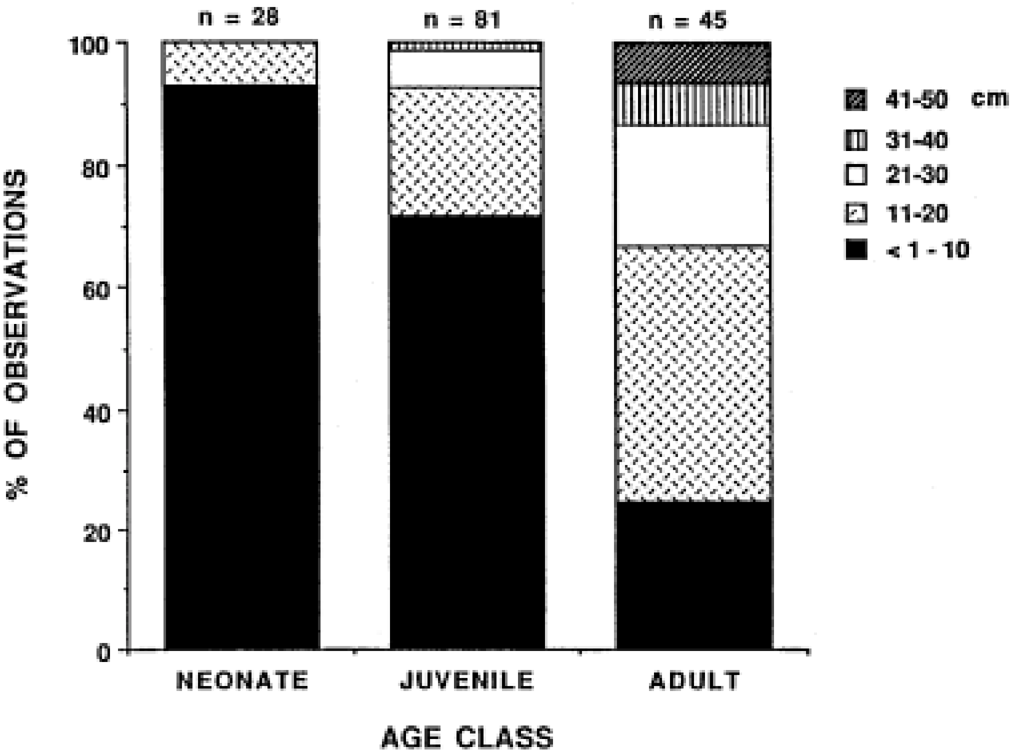


Figure 8. Use of Stream Water Depths by Three Age Classes of Snakes; Chi-sq = 46.76, p <0.0001, n = Total Number of Individuals Observed in Any Age Class.

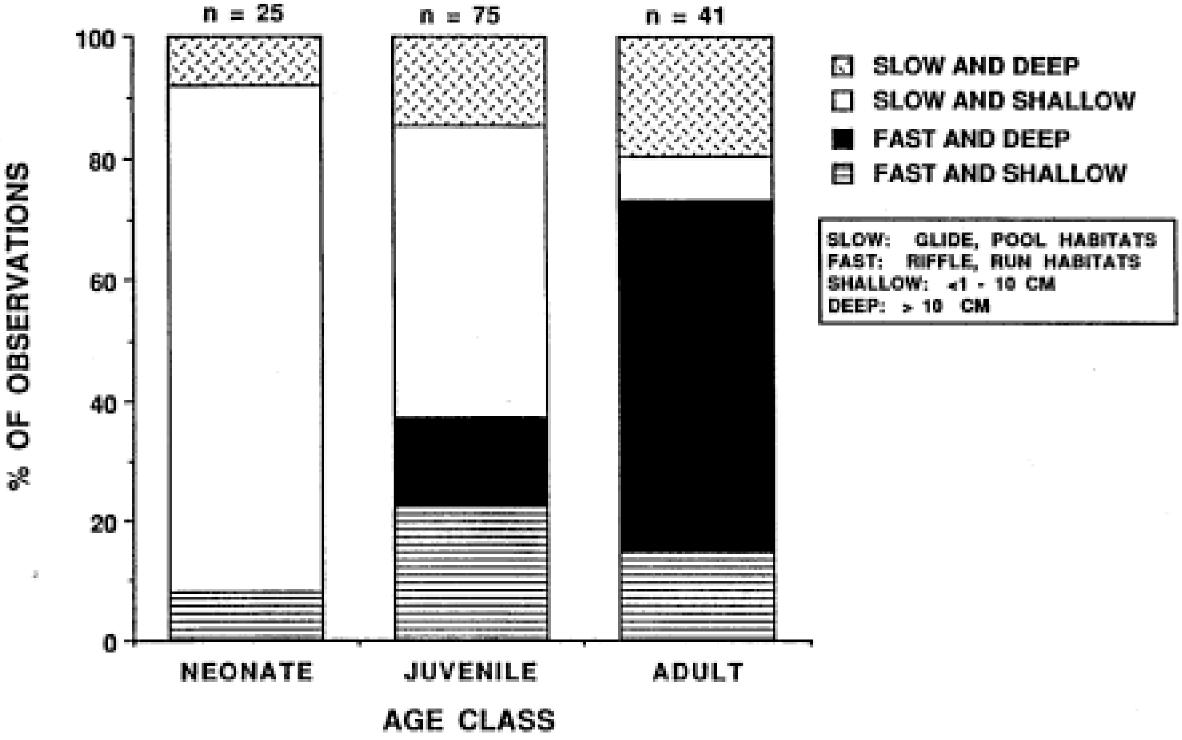


Figure 9. Use of Stream Habitat and Water Depth Combinations by Three Age Classes of Snakes; Chi-sq = 54.65, p <0.0001, n = Total Number of Individuals Observed in Any Age Class.

age classes, with juveniles having the highest proportion of full stomachs (37%), followed by adults (20%) and neonates (18%).

Differences in prey type and frequency among age classes were significant (Table 4). Once again there were several cells with low expected values (Appendix A). The diet of neonates and juveniles primarily consisted of tadpoles and fish (Fig. 10). Adults took a high proportion of larval and neotenic salamanders, but also took some fish and tadpoles (Fig. 10). These differences in prey type also represented a shift in prey size as snakes got older. The fish and tadpoles that made up the bulk of the diet of neonates and juveniles were relatively small; up to 50 mm total length (H. Welsh, unpublished data, USDA Forest Service, Redwood Sciences Lab, 170 Bayview Drive, Arcata. CA 95521). The larval and neotenic salamanders taken by the adults were relatively large; up to 133 mm SVL (Lind and Welsh 1990).

Attack Behavior and Foraging Success

Thirty-five foraging observations included attacks on prey; four by neonates, 22 by juveniles, and nine by adults. Three of four neonates attacked using ambush or craning behaviors, and the other attacked while substrate-crawling in a shallow riffle (Fig. 11a). Juveniles used a variety of foraging behaviors prior to attacks (Fig. lla). All adults attacked while underwater substrate-crawling; six of the nine adults were seen prior to attack, the other three were observed in the process of subduing prey so attack behavior could not be determined (Fig. 11a). Habitats where attacks occurred were similar to overall habitat use for each age class (Fig. llb and Fig. 7)

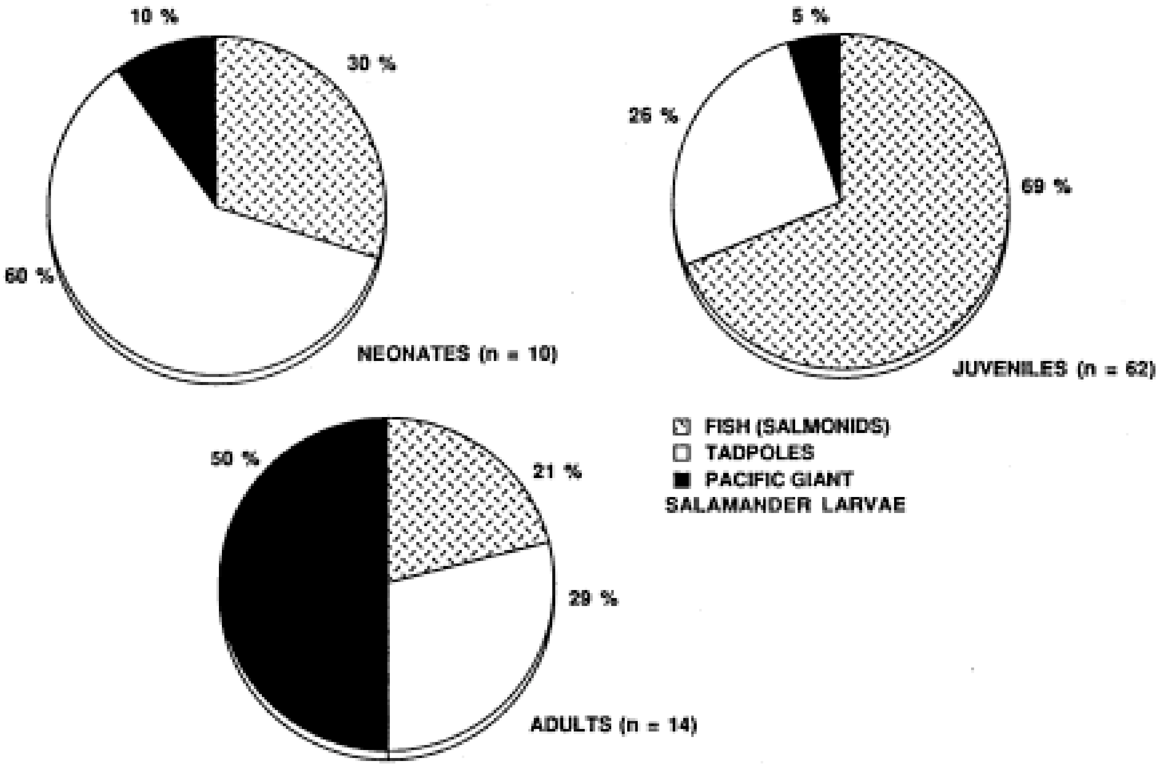


Figure 10. Stomach Contents of Snakes from 1987 and 1988 Monthly Censuses; Chi-sq = 27.68, p <0.0001, n = Total Number of Individuals in Any Age Class.

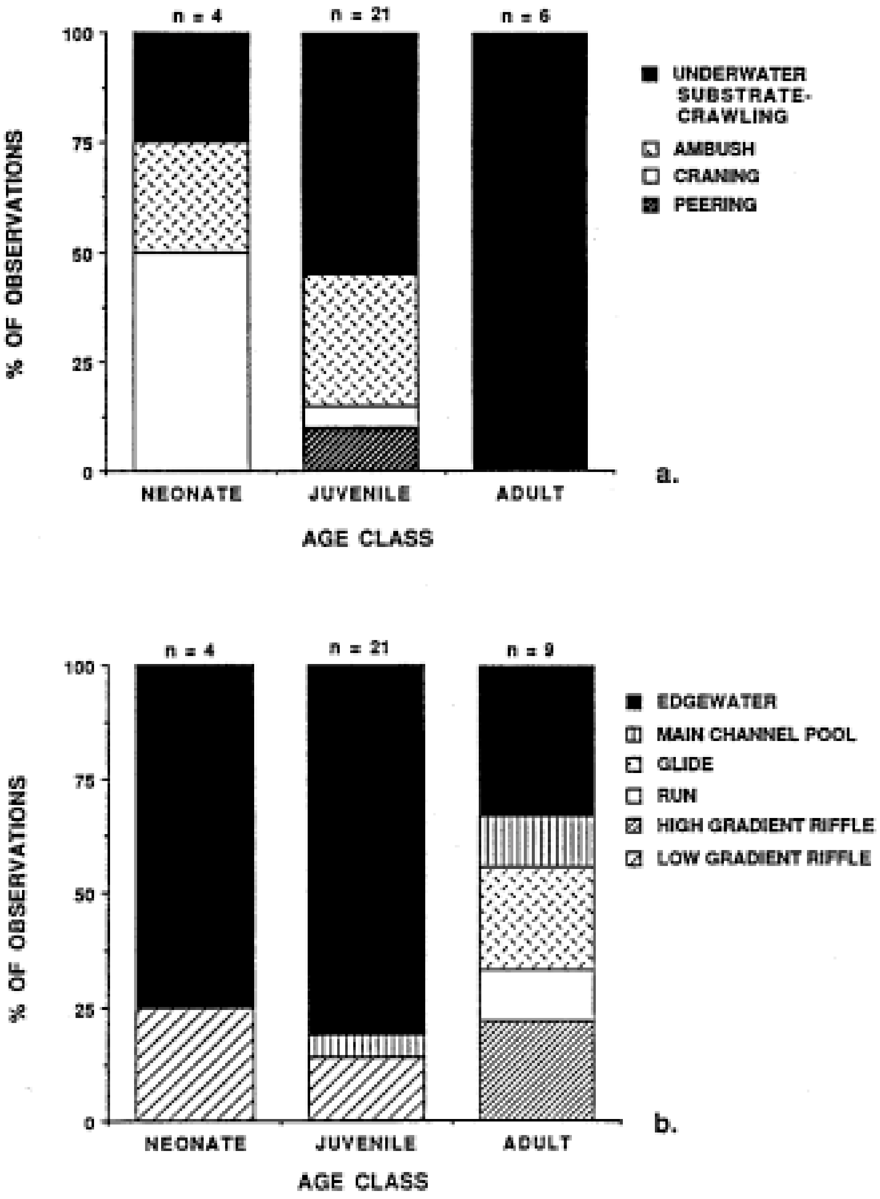


Figure 11. Pre-attack Behavior (a) and Attack Habitat (b) for Three Age of Snakes; n = Total Number of Individuals Observed in Any Age Class.

The proportions of prey types attacked were similar to food habits (Fig. 10 and Fig. 12a). Unknown prey were those that could not be positively identified (i.e., an attack behavior was seen, but no prey was seen). Prey attack success rate was highest among adults and no successful attacks were observed for neonates (Fig. 12b). Even though sample sizes are small, it is reasonable to speculate that this is due to foraging experience.

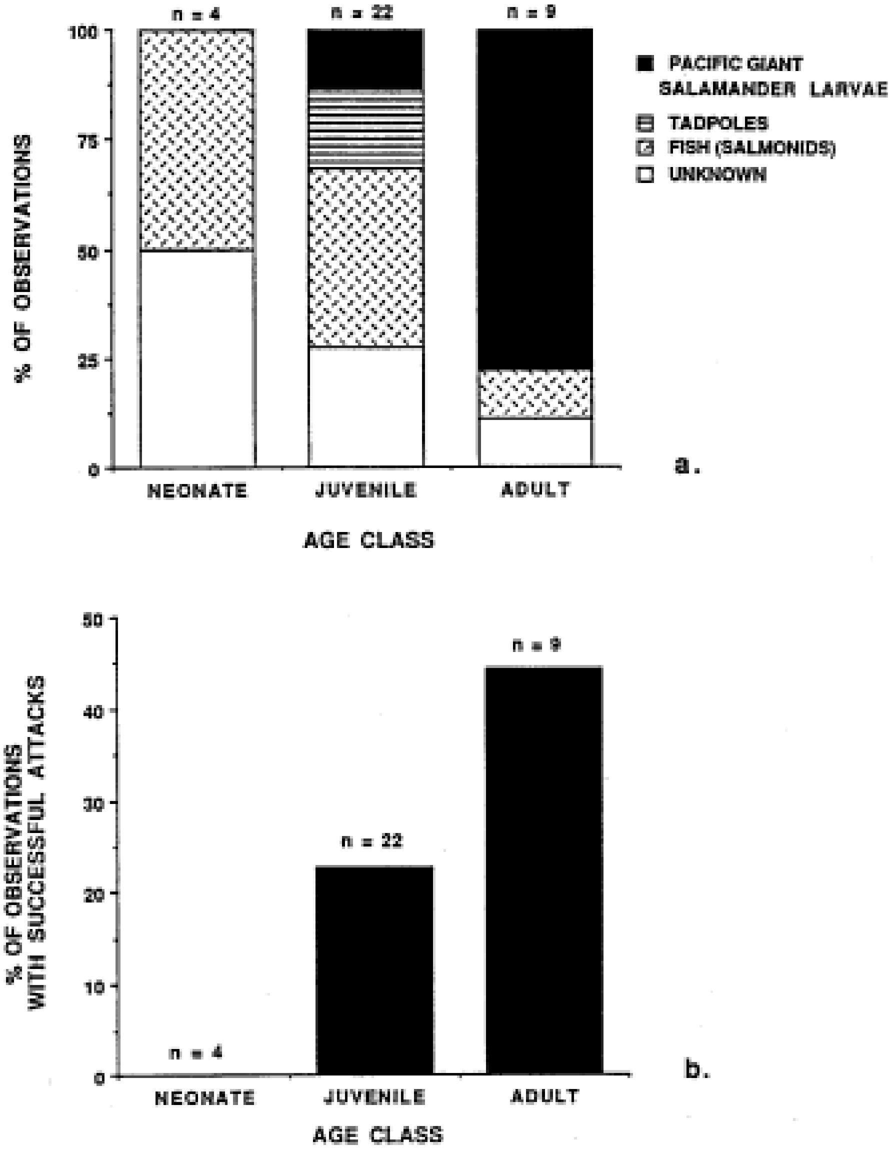


Figure 12. Prey Attacked (a) and Attack Success Rate (b) of Three Age Classes of Snakes; n = Total Number of Individuals Observed in Any Age Class.

DISCUSSION

Foraging Behaviors of Aquatic Garter Snakes and Water Snakes

Drummond (1983) studied the behaviors of *Thamnophis couchii* and other species of garter snakes and a species of water snake *Nerodia* spp.). Laboratory (n = 8 individuals) and field observations (n = 3 individuals) of small juvenile *T. couchii* foraging for fish indicated that they spent the greatest proportion of their time underwater substrate-crawling and that most prey were attacked from this position (Drummond, 1983). Though this appears to be in conflict with my results, I found that juveniles used a combination of sit-and-wait and active foraging behaviors, Drummond's results probably were influenced by his small sample sizes and the fact that he only observed snakes foraging for one prey type (small fish - minnows, mosquito fish, and dace). There also could be differences in foraging behaviors among populations of western aquatic garter snakes.

Drummond (1983) also found that juvenile *Thamnophis melanogaster*, another aquatic-foraging garter snake, and juvenile *Nerodia sipedon*, used underwater substrate-crawling in both laboratory and field studies. In addition, *N. sipedon* used underwater open-mouth searching, and craning behaviors with dives to attack fish. Studies of other species of *Nerodia* have described the "underwater open-mouth search" behaviors as common though the possibility of ontogenetic changes in behavior were not considered (Evans, 1942; Gillingham and Rush, 1974; Mushinsky and Hebrard, 1977).

Ontogentic Shifts in Foraging Mode, Stream Habitat Use and Food Habits

My results provide strong evidence of ontogenetic changes in foraging behavior, stream habitat use, and food habits in western aquatic garter snakes. Comparisons of these variables among three age classes indicated that adults moved at a faster rate (Fig. 4) and used more active foraging behaviors than either juveniles or neonates (Figs. 5 and 6). Adults also used a wider variety of stream habitats and water depths than the other age classes (Figs. 7,8,9). Food habits also differed among age classes (Figs. 10). Neonates and juveniles primarily fed on young of the year salmonids and tadpoles inhabiting stream margins (Fig. 10). Adults fed on these prey, but also took large larval and neotenic pacific giant salamanders, which are main channel substrate dwellers (Fig. 10). Attack behaviors and foraging success appeared to differ (Figs. 11 and 12), though sample sizes were too small to test.

The differences observed in overall foraging mode need to be examined in the context of the ecological factors affecting this population. Habitat structure, ambient temperatures, prey availability, exposure to predation, and resource partitioning probably act in concert with morphological and physiological constraints (e.g., jaw size, mobility and strength, buoyancy control, and thermal requirements) to influence which foraging mode was used by each snake age class. Some of these factors have been examined by others for related species of snakes as well as lizards (Huey and Pianka, 1981; Voris and Moffet, 1981; Pough and Andrews, 1985; Stevenson et al. 1985).

Prey Availability and Predation

Huey and Pianka (1981) provided insight into the potential advantages and disadvantages of sit-and-wait foraging versus "widely foraging" (active) for several species of desert lizards. Prey type and frequency of exposure to predation were directly related to foraging mode for any given species, although some intraspecific shifts in foraging mode were observed and were attributed to fluctuations in prey availability. However, they also noted the importance of morphology and physiology as factors limiting "the flexibility of foraging mode".

Prey availability and exposure to predation also may be important factors for western aquatic garter snakes (Table 1). The ontogenetic shift in diet from relatively small prey for young snakes to relatively large prey for adult snakes may be a result of an advantage gained by foraging less often for larger prey. Foraging less often may result in less exposure to predators (Huey and Pianka, 1981; Lind and Welsh, 1990). This idea is confounded by the fact that adult snakes forage more actively and large meals usually reduce snake mobility (Garland and Arnold, 1983; Lind and Welsh, 1990), resulting in increased vulnerability of the snakes to predators. The foraging mode of predators on snakes must also be considered. For example, sit-and-wait foraging neonates may be targets of active predators like soaring or wading birds (Table 1), while large adults foraging underwater may not be visible to these same predators.

These complex questions require carefully designed experiments in which each factor can be controlled at each trophic level. Even so, explanations based solely on prey availablility and exposure to predators ignore morphological and physiological limitations on foraging which Huey and Pianka (1981) and others (Greene, 1983; Stevenson et al., 1985) considered important.

Physiological Limitations and Habitat Use

Aquatic foraging snakes are confronted daily with fluctuating temperatures and the difficulty of foraging in moving water. All aspects of snake physiology are affected by temperature (Stevenson et al., 1985) and snakes must compensate for thermal fluctuations experienced when moving between land and water. Body temperatures of small snakes change more quickly than large snakes when exposed to changes in ambient temperatures (C. Peterson, pers. comm., Dept. of Biology, Box 8007, Idaho State University, Pocatello, ID 83209). This aspect of physiology could influence the frequency of use of active, underwater foraging behaviors by small snakes, although it may be a seasonal effect.

Foraging in moving water requires buoyancy control, strong swimming ability, and endurance. These abilities are likely to change as snakes grow. Drummond (1983) reported that his laboratory juvenile western aquatic garter snakes study could achieve negative buoyancy by expelling air, but his study was conducted in a pool of still water. Pough (1977, 1978) found significant differences in endurance of neonate and adult garter snakes (Thamnophis sirtalis) and water snakes

(Nerodia sipedon). He found that adults could sustain maximum activity for five to eight times longer than neonates and suggested that the physiological characters of small snakes limited the types of foraging behaviors they could use and the habitats in which they could forage. Ontogenetic changes in these factors might explain the differences I observed in the use of stream habitats. Neonate and juvenile T. couchii foraged mainly in shallow, quiet water; adults foraged in deeper, faster moving water (Figs. 7,8,9). I know of no studies that have addressed the question of ontogenetic changes in habitat use for garter snakes, but Tiebout and Cary (1987) and Scott et. al (1989) noted this in species of water snakes (Nerodia spp.). Specifically, Scott et al. (1989) reported that adults of three species of water snakes were found more frequently in deep water than were juveniles.

Food Habits and Resource Partitioning

Another possible explanation for ontogenetic changes in foraging modes is resource partitioning. Food and habitat partitioning among sympatric species (Carr and Gregory, 1976; Mushinsky and Hebrard, 1977; Hebrard and Mushinsky, 1978) and ontogenetic shifts within species (Mushinsky et al. 1982; Plummer and Goy, 1984) have been studied in Nerodia spp. Resource partitioning was observed in these studies, but some overlap in habitat use or diet also occured among species or among size classes within species. In my study, the food habits of neonate, juvenile and adult snakes differed markedly, but no prey type were taken exclusively by one age class (Fig. 10). This overlap in diets among age classes may be a result of differing prey availability throughout spring and summmer and from year to year (Kephart and Arnold, 1982; Garcia and Drummond, 1988). One possible explanation for an ontogenetic dietary shift, is the habitat of the prey. Small fish and tadpoles are generally found in stream margins and large larval and neotenic salamanders are usually found in the main channel of the stream inhabiting substrate crevices. If snakes are only physiologically able to forage in certain habits, they would only encounter certain prey.

Gape and head size also limit the size of prey that can be taken. Small snakes can only swallow prey up to their maximum gape, and though large snakes can swallow small prey, they may not be able to forage in small crevices that some small prey inhabit (Voris and Moffett, 1981; Greene, 1983).

Dietary shifts also may be evidence of an overall shift in foraging "strategy"; from feeding frequently on small prey to feeding infrequently on large prey (Lind and Welsh, 1990). Such a shift may be facilitated by a change in foraging mode from sit-and-wait to active, if there were advantages to eating large prey items instead of, or in addition to, small ones. Before concluding that resource partitioning is a factor in this system, a more detailed look at prey type and size relative to snake size is needed. Studies of seasonal and yearly fluctuations in prey abundance, and an examination of other aquatic foraging animals (e.g., dippers, otters, etc.) that may compete with the western aquatic garter snake (Table 1) are also needed.

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Appendix A. MINITAB (1988) Output from Chi-Square Contingency Table Analysis. Tables Show Observed and Expected Values. Chi-square Values for Each Cell and Overall are Given Below Each Table.

BEHAVIOR (8 TYPES) AND AGE CLASS

```
Expected counts are printed below observed counts

              JUV       ADL       NEO      Total
BASKING        19        11         4        34
            17.88      9.94      6.18

PEERING        23        12         3        38
            19.99     11.10      6.91

CRANING         5         1         2         8
             4.21      2.34      1.45

CRUISING        3         3         2         8
             4.21      2.34      1.45

AMBUSH         18         0        12        30
POS.        15.78      8.77      5.45

SUBSTRATE-      5        13         0        18
  CRAWLING   9.47      5.26      3.27

ATTACK/         3         3         1         7
FEEDING      3.68      2.05      1.27

MARGIN-         5         2         4        11
WANDER       5.79      3.21      2.00

Total          81        45        28       154

ChiSq = 0.070 +  0.114 + 0.770 +
        0.454 +  0.072 + 2.212 +
        0.149 +  0.765 + 0.205 +
        0.347 +  0.188 + 0.205 +
        0.313 +  8.766 + 7.855 +
        2.108 + 11.391 + 3.273 +
        0.126 +  0.445 + 0.058 +
        0.107 +  0.459 + 2.000 = 42.451
df = 14
12 cells with expected counts less than 5.0
```

Appendix A. MINITAB (1988) Output from Chi-Square Contingency Table Analysis. Tables Show Observed and Expected Values. Chi-square Values for Each Cell and Overall are Given Below Each Table. (continued)

FORAGING MODE AND AGE CLASS

```
Expected counts are printed below observed counts

          JUV     ADL     NEO    Total
SIT &      31       0      21      52
WAIT    27.39   15.08    9.53

ACTIVE     26      37       2      65
        34.24   18.85   11.91

BOTH       12       1       1      14
         7.37    4.06    2.56

Total      69      38      24     131

ChiSq =  0.476 + 15.084 + 13.818 +
         1.982 + 17.462 +  8.244 +
         2.902 +  2.307 +  0.955 = 63.229
df = 4
2 cells with expected counts less than 5.0
```

Appendix A. MINITAB (1988) Output from Chi-Square Contingency Table Analysis. Tables Show Observed and Expected Values. Chi-square Values for Each Cell and Overall are Given Below Each Table. (continued)

```
      HABITAT AND AGE CLASS

Expected counts are printed below observed counts

         JUV     ADL     NEO     Total
LOW GRAD. 24      14       2     40
RIFFLE 21.04   11.69    7.27

HIGH GRAD. 2       5       0     7
RIFFLE  3.68    2.05    1.27


RUN        2      11       0     13
        6.84    3.80    2.36


GLIDE      3       4       0      7
        3.68    2.05    1.27


MID-CHANNEL 2      2       0      4
POOL    2.10    1.17    0.73

EDGEWATER 42       5      23     70
POOL   36.82   20.45   12.73

ON SHORE   6       4       3     13
        6.84    3.80    2.36

Total      81      45      28    154

ChiSq = 0.417 +  0.457 + 3.823 +
        0.768 +  4.268 + 1.273 +
        3.423 + 13.652 + 2.364 +
        0.126 +  1.868 + 1.273 +
        0.005 +  0.591 + 0.727 +
        0.729 + 11.677 + 8.292 +
        0.103 +  0.011 + 0.171 = 56.016
df = 12
* WARNING * 1 cells with expected counts less than 1.0
          * Chisquare approximation probably invalid
13 cells with expected counts less than 5.0
```

Appendix A. MINITAB (1988) Output from Chi-Square Contingency Table Analysis. Tables Show Observed and Expected Values. Chi-square Values for Each Cell and Overall are Given Below Each Table. (continued)

WATER DEPTH AND AGE CLASS

```
Expected counts are printed below observed counts

          JUV     ADL     NEO    Total
 <1-10CM   58      11      26      95
         49.97   27.76   17.27

11-20CM    17      19       2      38

        19.99   11.10    6.91


21-30CM     5       9       0      14

         7.36    4.09    2.55


31-4ocM     1       3       0       4

         2.10    1.17    0.73


41-50CM     0       3       0       3

         1.58    0.88    0.55


Total      81      45      28     154


ChiSq = 1.291 + 10.119 + 4.410 +
        0.446 +  5.615 + 3.488 +
        0.759 +  5.891 + 2.545 +
        0.579 +  2.869 + 0.727 +
        1.578 +  5.143 + 0.545 = 46.006
df = 8
* WARNING * 3 cells with expected counts less than 1.0
          * Chisquare approximation probably invalid
8 cells with expected counts less than 5.0
```

Appendix A. MINITAB (1988) Output from Chi-Square Contingency Table Analysis. Tables Show Observed and Expected Values. Chi-square Values for Each Cell and overall are Given Below Each Table. (continued)

HABITAT (LUMPED - FAST OR SLOW) AND AGE CLASS

```
Expected counts are printed below observed counts

          JUV     ADL     NEO    Total
FAST       28      30       2      60
MOVING  31.91   17.45   10.64

SLOW       47      11      23      81
MOVING  43.09   23.55   14.36

Total      75      41      25     141

ChiSq = 0.480 + 9.032 + 7.014 +
        0.356 + 6.690 + 5.196 = 28.769
df = 2
```

WATER DEPTH (LUMPED - DEEP AND SHALLOW) AND AGE CLASS

```
 Expected counts are printed below observed counts

          JUV     ADL     NEO    Total
 SHALLOW   57      11      26      94
        49.15   27.65   17.20

DEEP       23      34       2      59

        30.85   17.35   10.80

Total      80      45      28     153

ChiSq = 1.254 + 10.024 + 4.499 +
        1.997 + 15.970 + 7.168 = 40.911
df = 2
```

Appendix A. MINITAB (1988) Output from Chi-Square Contingency Table Analysis. Tables Show Observed and Expected Values. Chi-square Values for Each Cell and Overall are Given Below Each Table. (continued)

HABITAT/DEPTH INDEX AND AGE CLASS

```
Expected counts are printed below observed counts

          JUV     ADL     NEO   Total
FAST/      17       6       2      25
SHALLOW 13.30    7.27    4.43

FAST/      11      24       0      35
DEEP    18.62   10.18    6.21

SLOW/      36       3      21      60
SHALLOW 31.91   17.45   10.64

SLOW/      11       8       2      21
DEEP    11.17    6.11    3.72

Total      75      41      25     141


ChiSq = 1.031 +  0.222 +  1.335 +
        3.116 + 18.774 +  6.206 +
        0.523 + 11.963 + 10.092 +
        0.003 +  0.587 +  0.798 = 54.649
df = 6
2 cells with expected counts less than 5.0
```

Appendix A. MINITAB (1988) Output from Chi-Square Contingency Table Analysis. Tables Show Observed and Expected Values. Chi-square Values for Each Cell and Overall are Given Below Each Table. (continued)

```
    CENSUS STUDY FOOD HABITS AND AGE CLASS

Expected counts are printed below observed counts

          JUV     ADL     NEO     Total
FISH       43       3       3      49
        35.33    7.98    5.70

TADPOLES  16        4       6      26
       18.74    4.23    3.02

SALAMANDERS 3       7       1      11
         7.93    1.79    1.28

Total      62      14      10      86

ChiSq = 1.667 +  3.105 + 1.277 +
        0.402 +  0.013 + 2.931 +
        3.065 + 15.154 + 0.061 = 27.675
df = 4
4 cells with expected counts less than 5.0
```