Anim. Behav., 1994, **48**, 1261–1273

Ontogenetic changes in foraging behaviour and habitat use by the Oregon garter snake, *Thamnophis atratus hydrophilus*

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(Received 2 August 1993; initial acceptance 7 August 1993;
final acceptance 18 October 1993; MS. number: A6413R)

Abstract. Foraging behaviour, stream habitat use and food habits of a population of the aquatic, Oregon garter snake were studied in the field during the spring and summer of 1987 and 1988. Continuous records of behaviour and habitat use were obtained for each snake. Adults foraged more actively and in a wider variety of stream habitats than juveniles or neonates. Adults also fed on a wider variety of prey types and sizes, especially concentrating on large, Pacific giant salamander, *Dicamptodon tenebrosis*, larvae and neotenes, in the mid-stream substrates. Juvenile and neonate snakes fed on relatively smaller prey that inhabited shallow stream margins. Consumption of relatively large prey by adults and smaller prey by juveniles indicated a shift in foraging 'strategy' from frequent feeding on small prey to infrequent feeding on large prey. These ontogenetic changes in foraging behaviour, habitat use and food habits of Oregon garter snakes are probably the result of a combination of proximate ecological, morphological and physiological constraints. Ultimately, these behavioural shifts may have a phylogenetic origin that reflects the strong advantage of single large meals versus many small meals for many modern snake lineages.

Foraging and feeding behaviour comprise the primary defining attributes of predatory organisms in ecological (Morse 1980) and evolutionary contexts (Greene 1986). Ontogenetic changes in foraging behaviour and foraging modes (e.g. 'sit-and-wait' and active foraging; Schoener 1971) have rarely been studied in reptiles (Burghardt 1978; Mushinsky 1987), although understanding such shifts has important implications for animal learning, development, optimal foraging, phylogenetic systematics and evolution. For example, behaviour patterns are increasingly used as character states in phylogenetic analyses and lack of knowledge of the behaviour of different ages of snakes could result in faulty conclusions about phylogenetic relationships. Similar problems plague optimal foraging theory which typically has not reflected development of behaviour over time (Stephens & Krebs 1986; Stephens 1990). Finally, snakes were probably derived from a fossorial lizard or lizard-like ancestor (Rage 1987) that fed frequently on small prey (Greene 1982; Regal 1983). Changes in feeding behaviour have been proposed as a key development in the early evolution of snakes, with a trend towards the capture of larger prey leading to the derivation of many modern forms (Greene 1983). Studies of ontogenetic changes in feeding biology across a variety of taxa might clarify that scenario.

Some information is available on the foraging behaviour of snakes of the largest family, Colubridae (Arnold 1980; Drummond 1983; Drummond & Macias Garcia 1989; Jones 1990), and also the family Viperidae (Reinert et al. 1984; Duvall et al. 1985). Laboratory studies of *Thamnophis* and *Nerodia* spp. have provided categorizations of foraging behaviour along with important information on foraging in controlled settings (Drummond 1983, 1985; Halloy & Burghardt 1990). Studies of the food habits of several species of water snakes (Colubridae: *Nerodia* and *Regina* spp.) and sea snakes (Hydrophiididae) indicate that both size and type of prey change as snakes mature (Godley 1980; Voris & Moffett 1981; Mushinsky et al. 1982; Plummer & Goy 1984). In water snakes, prey size increases with snake size, whereas sea snakes take a wider range of prey sizes as they mature, but do not forage exclusively on larger prey. These studies

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indicate differential foraging among juvenile and adult snakes, but documentation of the constraints governing different behaviour patterns and foraging modes is limited (Huey & 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 snakes of different sizes (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 1991). Most species in the genus are diurnal, and many forage in open habitat, presenting excellent opportunities for field studies of foraging behaviour. The Oregon garter snake forages in and along streams (Fitch 1941; Stebbins 1985; nomenclature follows Rossman & Stewart 1987; Collins 1990). Aquatic garter snakes are primarily visual predators (Drummond 1985; Jones 1990; personal observations) and foraging in water adds another dimension to the ecological and physiological factors influencing behaviour. 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 (behavioural or physiological) probably exists that allows maintenance of preferred body temperatures (Burkett 1966; Fleharty 1967; Osgood 1970; Peterson 1987). Foraging in water also requires a mechanism to control buoyancy and breathing rate, in order to maximize efficiency.

Our aim was to describe and compare quantitatively the foraging behaviour, stream habitat use and food habits of three age (size) classes of Oregon garter snakes: neonates, juveniles and adults. We addressed the following questions. (1) Does the use of foraging behaviour and foraging mode vary among age classes? (2) Does use of stream habitats vary among age classes? (3) Do food habits differ among age classes? Information on attack behaviour and foraging success also was gathered. We examined age differences in foraging in the context of ecological factors, recognizing that there may also be important phylogenetic constraints (e.g. Arnold 1980) that our data cannot address.

STUDY AREA

Field work was conducted on the lower 5 km of Hurdygurdy Creek in Del Norte County, CA, U.S.A., at 200–250 m elevation. Hurdygurdy Creek is a third–fourth order (Strahler 1952) tributary of the south fork of the Smith River, ranging from 10 to 15 m wide, and contains typical lotic habitats (riffles, runs, pools, cascades, etc.) with predominantly cobble and boulder-sized substrate. There is a fairly narrow, though quite variable, zone of riparian vegetation (5–25 m) consisting of alders, *Alnus* spp., willows, *Salix* spp., and big leaf maple, *Acer macrophyllum*. Upland vegetation is dominated by Douglas fir, *Pseudotsuga menziesii*, and California laurel, *Umbellularia californica*. Summer high air temperatures range from 25 to 35°C and winter lows from 8 to 13°C. Water temperatures during this study ranged from 13 to 21°C. Winter rainfall is heavy, averaging 280 cm (range=152–330 cm). Historical land use in the Hurdygurdy Creek Basin has been primarily logging and mining (M. Furniss, personal communication, USDA Forest Service, Six Rivers National Forest, 1330 Bayshore Way, Eureka, CA 95501, U.S.A.).

METHODS AND ANALYSIS

Background

We began a study of food habits, habitat associations, and demographics of the Hurdygurdy Creek population of Oregon garter snakes in the summer of 1986. The study included monthly censuses (May–September) of an approximately 5-km section of the stream and provided a marked population of snakes (hereafter referred to as the census study). The census study provided background information on activity periods and stream habitat associations of the snakes. We used data on food habits collected during the census study from 1987 to 1988 because these data provided better sample sizes than similar data collected during behavioural observations.

Behavioural Observations

We observed snakes from May to September in 1987 and 1988, between 0900 and 1800 hours, the

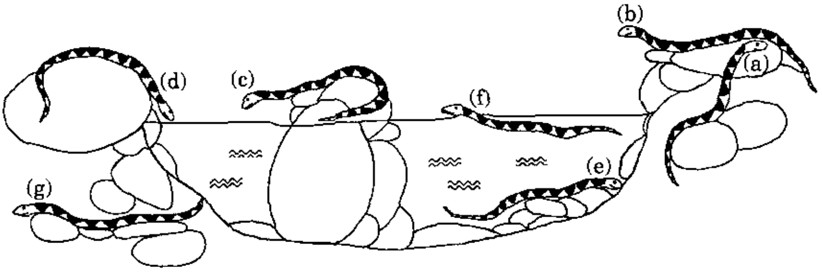

Figure 1. Behaviour of Oregon garter snakes observed at Hurdygurdy Creek, Del Norte county, California (modified from Drummond 1983). Inactive non-foraging: (a) basking/resting: lying mostly out of the water; head not oriented towards the water; (b) peering: head is well above the water but oriented towards it. Sit-and-wait foraging: (c) craning: body out of the water; head extended out over the water; tongue-flicking; (d) ambush position: body out of water; head oriented towards water, within a few centimetres of it; tongue-flicking. Active foraging: (e) underwater substrate-crawling: body completely submerged; crawling along stream bottom; probing in crevices; tongue-flicking. Active non-foraging: (f) cruising: body floating near water surface; head out of water; used to get from place to place; (g) margin-wandering: body out of water, on shore; crawling on substrate to get from place to place.

primary period of activity (personal observation). A portable data collector (PDC), OmniData Polycorder 601, was used to record observations of snakes along the stream (e.g. Hensler et al. 1986). The PDC has a built-in clock and was programmed to record changes and durations of behaviour and stream habitat use. The result was a continuous, sequential, account of an individual's activities. We observed individual snakes for as long as possible, however, 1 min was the minimum observation length used for analysis.

Behaviour patterns were defined with an emphasis on foraging behaviour and included: 'peering', 'craning', 'underwater substrate-crawling' and 'margin-wandering' (after Drummond 1983; Fig. 1). We used 'cruising' to describe snakes that were actually moving across the water surface, whereas Drummond used it 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. We included two additional categories, 'basking/resting' and 'ambush position'. We omitted two behaviour patterns described by Drummond, 'underwater open-mouth search' and 'serpentine dives', because they were not seen in our population. This may be because the Oregon garter snake, like other aquatic specialists, does not use these behaviour patterns (Drummond 1983; Drummond & Macias Garcia 1989). Other dives (anterior and mid-water) were seen only during attacks from stationary positions and were called 'attacks' and not separated into dive types. We categorized behaviour 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. 1). 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. Stream habitats were simplified from a detailed set of types designed for fisheries research (Table I).

We observed snakes that were underwater or appeared occupied with an activity from short distances (1–5 m) because they were not easily disturbed. We observed inactive snakes 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 towards the observer, moved its head quickly from side to side, and tongue-flicked. At the first sign of this behaviour, observations were terminated. At the end of each observation period the snake was captured, if possible, and the following data were collected: date, air and water temperature (°C) (proximal to the snake), amount of cloud cover, gender, snout–vent and total lengths (mm), weight (g), head diameter at widest point (mm), distance moved during the observation (visually estimated, to the nearest 0·1 m), water depth for snakes in or oriented towards the water (five depth classes: <1–10, 11–20, 21–30, 31–40 and 41–50 cm), location in the study area, and stomach contents (collected by palping, see Fitch 1987 for methods). All unmarked snakes

Table I. Descriptions of stream habitat types and frequency of use of types by three age classes of snakes at Hurdygurdy Creek, Del Norte County, California (types modified from Bisson et al. 1981; McCain et al. 1990)

Habitat type	Description	% Observations		
		Neonate	Juvenile	Adult
Low gradient riffle	Relatively shallow areas (10–50 cm)* with turbulent water and exposed substrate. Gradient is less than or equal to 4% and substrate is mostly pebble and cobble†	7·2	29·6	31·1
High gradient riffle	Relatively deep areas (10–50 cm) with swift flows, very turbulent water and large amounts of exposed substrate. Gradient is greater than 4% and substrate is mainly boulder	0·0	2·5	11·1
Run	Moderately deep areas (20–100 cm) with swift flows, but few flow obstructions, and little to no turbulence. Substrates are usually gravel, pebble, cobble and boulder	0·0	2·5	24·4
Glide	Wide, relatively shallow areas (30–90 cm), with low to moderate flow rate and no surface turbulence. Substrate is usually sand, gravel, pebble and cobble	0·0	3·7	8·9
Mid-channel pool‡	Large, relatively deep (90–240 cm) pools formed by mid-channel scour. Water velocity is slow, with variable substrates	0·0	2·5	4·5
Edgewater	Relatively shallow areas (10–40 cm) with little or no flow, in stream margins. They are often found associated with main channel riffle habitat, but small amounts occur along nearly all main channel stream habitats. Substrate is mainly pebble, cobble and boulder	82·1	51·8	11·1
On shore	Used for snakes moving along the stream bank and not obviously using or oriented towards a particular stream habitat type	10·7	7·4	8·9

*Depth ranges are from M. McCain (unpublished data, USDA Forest Service, Smith River National Recreation Area, P.O. Box 228, Gasquet, CA 95543, U.S.A.).

†Substrate size class diameters in mm (Lane 1947): sand: 0·0625–1·0; gravel: 1·0–32·0; pebble: 32·0–64·0; cobble: 64·0–256·0; boulder: greater than 256·0.

‡All pools other than edgewaters were categorized as mid-channel pools because snakes rarely used these habitats. A more refined system is available in Bisson et al. (1981) and McCain et al. (1990).

were given unique numbers when captured (Ferner 1979; Fitch 1987). For snakes that escaped capture (14·3% of observations), we estimated age/size class.

Analysis

Data collected from 3 years of monthly censuses were used to determine age/size classes. Snakes were considered neonates from parturition (usually in August or September) until they sought winter cover (usually 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 had snout–vent lengths of greater than or equal to 450 mm, 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 our census data and (3) evidence of size at maturity for other species of *Thamnophis* (White & Kolb 1974; Macias Garcia & Drummond 1988; Jayne & Bennett 1990). Adults with a snout–vent length of 450 mm are probably 2·5–3 years old. This size class break was used for both males and females, although males probably mature at a smaller size.

To assure independence of behavioural observations, we individually marked each snake, made observations throughout the census study area (e.g. no areas were sampled exclusive of others) and used the individual as the unit of analysis.

Each sequential observation of an individual was considered to be a single observation and lengthy observations were not broken into smaller segments to increase sample size. Only six of 132 captured and marked snakes were observed twice, and in each case these observations were at least 1 month apart. We do not know whether snakes that escaped capture ($N=22$) were observed more than once.

We used linear regression to relate rate of movement to size (SVL) of snakes. We corrected estimated distances for the length (in min) of the observation, resulting in a rate (m/min). Two variables were used in all other tests for differences in behaviour pattern and habitat use between snake age classes: (1) foraging mode and (2) a variable combining stream habitat and water depth. We derived the first variable by categorizing each observation (all behaviour patterns in the sequence for a given individual) as one of three general foraging modes: sit-and-wait, active, or a combination thereof (Fig. 1). The second variable combined habitats (Table I) into two categories, slow moving (glides, mid-channel pools, and edgewaters) and fast moving (low- and high-gradient riffles and runs), and water depth into two categories, shallow (<1–10 cm) and deep (>10 cm). We examined all possible combinations of these categories: shallow and slow, shallow and fast, deep and slow, and deep and fast. This combination variable provided a way to analyse two related physical aspects of the stream habitat as one variable, a habitat/water depth index. Analyses of the complete array of categories of behaviour, habitat and water depth are not presented here because contingency tables in which more than 20% of expected values equal five or less may provide biased results (Zar 1984, page 70), and these variables demonstrated such an arrangement (see Lind 1990 for more detailed treatments).

We tested for annual and gender differences in foraging mode and habitat use for each age class using chi-squared contingency table analysis. We found none, so data were combined for 1987 and 1988 and for males and females. We used chi-squared contingency table tests for association (independence) to evaluate the relationship between (1) snake age class and foraging mode and (2) snake age class and the habitat/water depth index. We also examined food habits data from 1987 and 1988 censuses for differences between snake age classes using chi-squared tests. Only snakes with stomach contents were included. For all chi-squared analyses the $P \leq 0\cdot05$ significance level was used to indicate a relationship of dependence between snake age and the variable of interest. Observations of prey attacks are presented descriptively because of small sample sizes among age classes. Attack success rate was defined as the proportion of individuals in an age class that attacked and successfully captured a prey item. It does not reflect multiple observations of one individual.

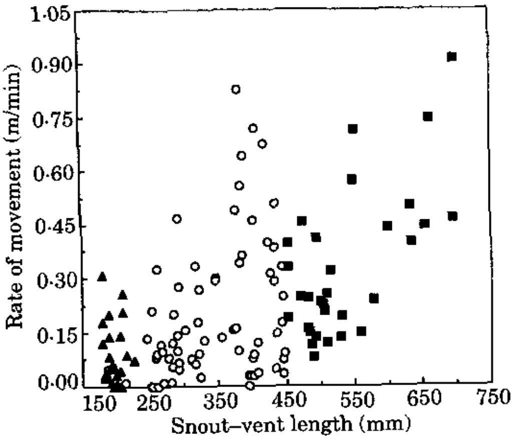

Figure 2. The relationship between rate of movement and size of snakes by age class. ▲: Neonates; ○: juveniles; ■: adults.

RESULTS

During the spring through late summer of 1987 and 1988, we made 154 behavioural observations on individuals in three age classes of Oregon garter snakes. The total observation time was 32·4 h and average durations of observations differed slightly among age classes (Table II).

Foraging Behaviour and Stream Habitat Use

Larger snakes moved at a greater rate than smaller snakes ($r^2_{\mathrm{adj}}=0\cdot313$, $F=59\cdot67$, $P=<0\cdot0001$; Fig. 2). Mean (±SD) rates of movement by age classes were: 0·08 ± 0·09 m/min (neonates); 0·22 ± 0·24 m/min (juveniles); and 0·44 ± 0·73 m/min (adults). All three age classes of snakes were seen to use all patterns of behaviour

Table II. Summary of behavioural observations of Oregon garter snakes by age class at Hurdygurdy Creek (Del Norte County, California) in 1987 and 1988

		Sex			Mean		Mean (± SD) observation
Age class	*N*	F	M	U	SVL (mm)	Mass (g)	duration (min)
Neonates	28	17	9	2	196·3 (179–226)	3·3 (1·7–5·00)	14·3 ± 6·9 (4·50–37·20)
Juveniles	81	41	32	8	341·9 (188–446)	16·9 (3·5–44·0)	12·9 ± 8·8 (1·97–46·17)
Adults	45	16	17	12	537·6 (451–700)	65·1 (30·0–184·0)	11·1 ± 11·8 (1·47–82·00)
All	154	74	58	22	362·2 (179–700)	25·6 (1·7–184·0)	12·6 ± 9·5 (1·47–82·00)

F: Female; M: male; U: unknown (escaped snakes).
Ranges are given in parentheses.

(Fig. 1) at some time during the study. Foraging mode was significantly associated with age (χ^2=62·23, P<0·0001). Neonates generally used sit-and-wait behaviour, adults used mainly active behaviour, and juveniles used combinations of both (Fig. 3). The primary differences were in the use of ambush and underwater substrate-crawling. Neonates most often used an ambush position for foraging. Juveniles used both ambush and underwater substrate-crawling. Adults used underwater substrate-crawling almost exclusively (Fig. 3). Other non-foraging behaviour patterns such as basking and margin-wandering were used equally among age classes.

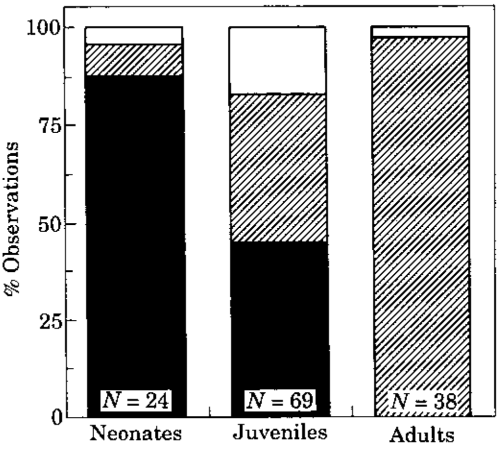

Figure 3. Frequency of foraging modes used by three age classes of snakes; ■: sit and wait; ▨: active; □: combination. N=Total number of individuals observed.

Frequency of use of the combined habitat and water depth categories were significantly associated with age class (χ^2=40·91, P<0·0001). The most striking differences were between neonates and adults, with juveniles falling in between (Table I, Fig. 4). Neonates were the most specialized; more than 80% were found associated with shallow (<10 cm) edgewaters. Adults were found mainly in fast-moving water with depths up to 0·5 m, and juveniles were found in relatively shallow riffles and edgewaters (Fig. 4).

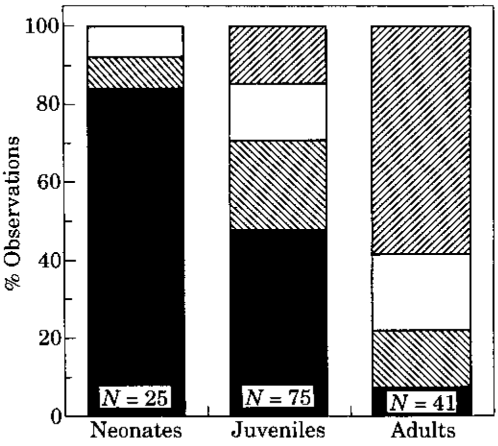

Figure 4. Frequency of stream habitat and water depth combinations used by three age classes of snakes; ■: shallow and slow; ▧: shallow and fast; □: deep and slow; ▨: deep and fast. N=Total number of individuals observed.

Table III. Stomach contents of Oregon garter snakes by age class from monthly censuses at Hurdygurdy Creek (Del Norte County, California) in 1987 and 1988

	Stomach contents				
Age class	Fish	Tadpoles	Pacific giant salamander larvae	Empty	Total
Neonates	3 (30%)	6 (60%)	1 (10%)	46	56
Juveniles	43 (69%)	16 (26%)	3 (5%)	104	166
Adults	3 (21%)	4 (29%)	7 (50%)	58	72

The number of individuals in each category represent total counts. Percentages are based on stomach contents of snakes that consumed food items.

Table IV. Attack success rate by prey type for three age classes of Oregon garter snakes from behavioural observation at Hurdygurdy Creek (Del Norte County, California) in 1987 and 1988

	Prey type				
Age class	Fish	Tadpoles	Pacific giant salamander larvae	Unknown	Total
Neonates	2	0	0	2	4
	0	—	—	0	0 (0%)
Juveniles	9	4	3	6	22
	2	1	2	0	5 (23%)
Adults	1	0	7	1	9
	0	—	4	0	4 (44%)

Counts are given in stacked pairs: the upper number represents the number of attacks observed; the lower number represents the number of times an attack was successful. Total (percentage) successful attack rate is given in the last column.

Food Habits

Of 294 snakes captured during the 1987 and 1988 censuses, 86 (29·3%) had stomach contents. The proportion of full stomachs differed among age classes, with juveniles having the highest proportion of full stomachs (37%), followed by adults (20%) and neonates (18%). Differences in prey type frequency among age classes were significant ($\chi^2=27{\cdot}68$, $P<0{\cdot}0001$). The diets of neonates and juveniles consisted primarily of tadpoles and fish (Table III). Adults took a high proportion of larval and neotenic salamanders, but also some fish and tadpoles (Table III). 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 (less than 50 mm total length). The larval and neotenic salamanders taken by the adults were relatively large (up to 133 mm SVL) (Lind & Welsh 1990).

Attack Behaviour 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, and one attacked while substrate-crawling in a shallow riffle. Juveniles used a variety of foraging behaviour patterns prior to attacking. All adults seen prior to attacks ($N=6$) were substrate-crawling. Habitats where attacks were seen corresponded closely to overall habitat use for each age class (see Table I).

The proportions of prey types attacked were similar to overall food habits for each age class (Tables III and IV). Unknown prey were those that could not be positively identified (i.e. an attack was seen, but no prey was observed). The success rate of attacks was highest among adults and no successful attacks were observed for neonates (Table IV). Even though sample sizes are small, it is reasonable to speculate that improved attack success is the result of increased foraging experience.

DISCUSSION

Foraging of Aquatic Garter Snakes and Water Snakes

Drummond (1983) studied the behaviour of *T. couchii* (an aquatic garter snake very closely related to our study species), three other species of garter snakes, and a water snake, *N. sipedon*. His laboratory ($N=8$ individuals) and field observations ($N=3$ individuals) of small juvenile *T. couchii* foraging for fish indicated that these snakes spend the greatest proportion of their time underwater substrate-crawling and that most prey are attacked from this position (Drummond 1983). In contrast, we found that Oregon garter snake juveniles used a combination of sit-and-wait and active foraging. Drummond's results were probably influenced by his small sample sizes and the fact that he observed snakes foraging for only one prey type (small fish: minnows, mosquito fish and dace) in pool habitats in contrast to our work in a lotic system. There could also be real differences in patterns of foraging behaviour between these closely related species because differences have even been seen among populations of other garter snakes (Drummond & Burghardt 1983; Macias Garcia & Drummond 1990).

Juvenile *T. melanogaster*, another aquatic-foraging garter snake, and juvenile *N. sipedon* were observed to use underwater substrate-crawling in both laboratory and field studies (Drummond 1983). In addition, Drummond observed *N. sipedon* to use underwater open-mouth searching and craning behaviour during dives to attack fish. Studies of other species of *Nerodia* have described the 'underwater open-mouth search' behaviour as common, although the possibility of ontogenetic changes in behaviour were not considered (Evans 1942; Gillingham & Rush 1974; Mushinsky & Hebrard 1977).

Ontogenetic Shifts in Foraging and Habitat Use

Oregon garter snakes undergo ontogenetic changes in foraging behaviour, stream habitat use and food habits. Comparisons of these variables among three age classes indicate that adults use more active foraging behaviour, a wider variety of stream habitats and successfully capture larger prey than either juveniles or neonates (Figs 2–4, Tables I, III and IV). A recent laboratory study of specialist and generalist *Thamnophis* foraging on fish indicated that capture, handling, and ingestion times can vary among species and age classes (Halloy & Burghardt 1990). In addition, neonates of all species were found to move more slowly and handle prey longer than adult snakes suggesting advantages gained from experience or maturity (Halloy & Burghardt 1990). A field study of the semi-aquatic black-necked garter snake, *T. crytopsis*, demonstrated ontogenetic shifts in predatory behaviour, with neonates exclusively using sit-and-wait behaviour and adults exhibiting both sit-and-wait and active behaviour (Jones 1990). In his laboratory study of neonate *T. sirtalis*, Arnold (1978) found direct evidence that food preference changed with experience.

Viewing our data from an ecological perspective best addresses the complex of interacting factors that determine how a snake forages. Habitat structure, ambient temperatures, prey availability, exposure to predation and resource partitioning probably act in concert with developmental, morphological and physiological constraints (e.g. jaw size, mobility and strength, buoyancy control and thermal requirements) to influence which foraging mode is used by each snake age class. Some of these factors have been examined by others for related species of snakes as well as for lizards (Godley 1980; Huey & Pianka 1981; Voris & Moffett 1981; Werner & Gilliam 1984; Pough & Andrews 1985; Stevenson et al. 1985). Phylogenetic considerations are also important in that they may influence the range of foraging 'strategies' available to individuals, populations, or entire species (Arnold 1980; Wcislo 1989; Jayne & Bennett 1990).

Prey availability and predation

Huey & Pianka (1981) discussed the potential advantages and disadvantages of sit-and-wait foraging versus 'widely foraging' (active) modes for several species of desert lizards. Prey types and frequency of exposure to predation were directly related to foraging mode for any given species, although some intraspecific shifts in foraging mode were attributed to fluctuations in prey availability. Prey densities affect foraging modes of

Chinese salamanders, *Cynops cyanurus* and *Cynops orientalis*, with more active searching behaviour used when densities are lower (Anthony et al. 1992). Huey & Pianka also noted the importance of morphology and physiology as factors limiting 'the flexibility of foraging mode'. It is important to recognize that these foraging modes are the endpoints of a continuum of foraging strategies and that using them as simple, rigid categories may not provide an accurate picture.

Prey availability and exposure to predation also may be important factors in limiting foraging mode of Oregon garter snakes. The ontogenetic shift in diet from relatively small prey for young snakes to relatively large prey for adult snakes may be related to differential encounter rates of prey of different sizes due to foraging mode or habitat (see Shine 1991). At Hurdygurdy Creek, small fish and tadpoles are generally found in stream margins, while large larval and neotenic salamanders are usually found in the main channel of the stream inhabiting substrate crevices. If small snakes, because of developmental constraints, are able to forage only in certain habitats, they may only encounter certain prey. Drummond & Macias Garcia (1989) suggested that differences in foraging abilities of generalist foragers and aquatic specialists would limit the type or stage of prey available to them.

Another possibility is that there are selective advantages gained by foraging less often for larger prey. Foraging less often may result in less exposure to predators (Huey & Pianka 1981; Greene 1983; Lind & Welsh 1990). However, adult snakes forage more actively, and large meals usually reduce snake mobility (Garland & Arnold 1983), resulting in increased vulnerability to predators if discovered. Our ontogenetic shift in predatory pattern parallels the comparable phylogenetic shift proposed by Greene (1983) for the adaptive radiation of modern snakes. We are not proposing here that ontogeny is recapitulating phylogeny, but the parallel is worth pondering. Both shifts may be a response to the availability of prey that infer a strong selective advantage, either in energetic terms or in terms of snakes avoiding predation, or both. In Oregon garter snakes such a shift would be facilitated by a change from sit-and-wait to active foraging which would increase both the rate of encounter of larger prey and success rate in capturing these prey. In general, smaller snakes have a higher per gram metabolic rate than larger snakes (Bennett & Dawson 1976) and thus would require relatively more prey than larger snakes, especially for growth. Ontogenetic shifts in foraging mode have been attributed to energetic constraints for an Australian skink, *Ctenotus taeniolatus* (Taylor 1986).

The foraging mode of predators on snakes must also be considered. For example, sit-and-wait foraging neonate snakes may be targets of active predators such as soaring or wading birds, whereas large adults foraging underwater may not be visible to these same predators. A number of potential predators inhabit our study area including river otter, *Lutra canadensis*, great blue heron, *Ardea herodias*, and Stellar's jay, *Cyanocitta stelleri*. However, explanations based solely on prey availability and exposure to predators ignore potentially important morphological and physiological limitations on foraging (Huey & Pianka 1981; Greene 1983; Stevenson et al. 1985; Toft 1985).

Physiological and morphological constraints

Stream foraging snakes are confronted daily with fluctuating temperatures and the difficulty of foraging in fast-moving water. All aspects of snake physiology are affected by temperature (Stevenson et al. 1985), and aquatic snakes must compensate for thermal fluctuations when moving between land and water. Body temperatures of small snakes change more quickly than those of large snakes when the snakes are exposed to changes in ambient temperatures. This aspect of physiology could influence the frequency of use of active, underwater foraging behaviour 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 juvenile western aquatic garter snakes in the laboratory 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 *T. sirtalis* and *N. sipedon*. He found that adults could sustain maximum activity for five to eight times longer than neonates and suggested that the physiological characteristics of small snakes limited the types of foraging behaviour they could use and the habitats in which they could forage. Ontogenetic changes in these physiological and morphological constraints might explain the differences we observed in the use of stream habitats. Neonate and juvenile Oregon garter snakes foraged mainly in shallow, quiet water; adults foraged in deeper, faster moving water. Jones (1990) found both seasonal and ontogenetic shifts in habitat use by *T. crytopsis*, and suggested it was related to physical changes in aquatic habitats and prey availability. Some water snakes (*Nerodia* spp.) also exhibit such shifts (Tiebout & Cary 1987; Scott et al. 1989; Manjarrez & Macias Garcia 1991). Scott et al. (1989) reported that adults of three species of water snakes were found more frequently in deeper water than were juveniles. There may also be selective factors acting in populations that facilitate the use of different habitats by larger (older) snakes. Recent work has indicated that selection may be acting to produce larger, faster individuals with greater endurance within a population of *T. sirtalis* (Jayne & Bennett 1990). For this species, however, it was hypothesized that increased survival rate based on these 'performance' characters was related more to improved ability to escape predation than to improved foraging success (Jayne & Bennett 1990).

Gape and head size also limit the size of prey that can be taken. Neonate and juvenile snakes would thus be limited to a smaller absolute prey size, and although large snakes can swallow small prey, they may not be able to forage in small crevices that some small prey inhabit (Voris & Moffett 1981; Greene 1983; Shine 1991). However, Miller & Mushinsky (1990) found, on the basis of a 'gape index', that large mangrove water snakes, *N. fasciata compressicauda*, actually ate relatively smaller prey than small water snakes.

Resource partitioning

Another possible explanation for ontogenetic changes in foraging modes is resource partitioning. In general, food is the primary resource partitioned in snakes. This appears to be an exception to most amphibians and reptiles that first partition habitat (Toft 1985). Partitioning of food and habitat and related ontogenetic shifts have been studied among sympatric species of *Nerodia* (Carr & Gregory 1976; Mushinsky & Hebrard 1977; Hebrard & Mushinsky 1978; Mushinsky et al. 1982; Plummer & Goy 1984). Resource partitioning was observed in these studies, but some overlap in habitat use or diet also occurred between species or between size classes within species. In our study, the food habits of neonate, juvenile and adult snakes differed markedly, but no prey types were taken exclusively by one age class (Table III). Overlap in diets between age classes may result from differing prey availability throughout spring and summer and from year to year (Godley 1980; Kephart & Arnold 1982; Macias Garcia & Drummond 1988; Jones 1990; King 1993).

Conclusions

We propose that an ontogenetic shift in foraging behaviour, prey selection and habitat use results from a tension between developmental constraints and an innate, possibly phylogenetically imposed, behavioural propensity on the part of the snakes to seek and capture larger prey. This propensity is the expression of a strong selective regime, particularly among diurnally active snakes, to limit foraging time and reduce exposure to predation by taking fewer, larger, prey (Huey & Pianka 1981; Greene 1983). Several lines of evidence indicate these factors are acting in the system we studied. Juvenile structural and physiological traits are often less developed than adults (Gould 1977; Thomson 1988) and this is true for natricine snakes (Pough 1977, 1978; Jayne & Bennett 1990). In addition, juvenile snakes have the ability and inclination to both underwater substrate-crawl and feed on smaller Pacific giant salamander larvae (Table III) that they can capture in stream margin habitats. As these snakes mature they show a greater propensity to actively forage (Figs 2 and 3) commensurate with increased motor skills (Pough 1977, 1978; Jayne & Bennett 1990). Thus it would appear that active patterns of foraging behaviour are present at birth (see also Drummond 1983). However, young snakes lack the ability, owing to developmental constraints, to successfully employ these behaviour patterns in the more turbulent water of the main channel. Not only does this habitat harbour larger salamanders, but it also conceals the foraging snakes from predators, providing a less risky foraging area than the more exposed shallow water along the stream margins. We also believe that structural and physiological development promotes improved diving ability by increasing tolerance to low water temperatures and increasing lung and blood oxygen capacity (cf. Pough 1977). This would increase buoyancy and breathing control and permit longer underwater foraging bouts.

The selective advantage of large prey for snakes is an evolutionary trajectory that has resulted in the radiation of many modern snake lineages (Greene 1983). Single large meals versus many small meals translates directly to less time exposed to predators while foraging. This advantage has probably been acting since the Cretaceous with the radiation of mammals and modern birds, both as predators (see Greene 1988 for a review) and prey (Greene 1983 and references cited therein).

ACKNOWLEDGMENTS

Portions of this research fulfilled requirements for a Master's Degree from Humboldt State University, Arcata, California, for the senior author. We thank D. Kitchen, G. Allen, C. Ralph, L. Fox, C. Zabel and two anonymous referees for helpful suggestions on early drafts. We are especially grateful to H. Greene for his suggestions and thorough review of this manuscript. Thanks also to J. Baldwin and D. Craigie for providing statistical advice and to K. Shimizu for help with figures. We thank L. Decker and M. McCain for providing habitat surveys and maps used to locate snakes within the study area. We are grateful to the Smith River National Recreation Area of the Six Rivers National Forest, California, USDA Forest Service, for providing field facilities for this project.

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