

HABITAT USE AND PREDATORY BEHAVIOR OF *THAMNOPHIS CYRTOPSIS* (SERPENTES: COLUBRIDAE) IN A SEASONALLY VARIABLE AQUATIC ENVIRONMENT

K. BRUCE JONES

*United States Environmental Protection Agency, Environmental Monitoring Systems Lab,
Post Office Box 93478, Las Vegas, NV 89193-3478*

ABSTRACT—Predatory behavior and habitat use were determined for *Thamnophis cyrtopsis* (black-necked garter snake) along two desert streams in western Arizona as part of a more comprehensive survey by the U.S. Bureau of Land Management to determine habitat uses of vertebrates on public lands. *Thamnophis cyrtopsis* appeared to vary its feeding behavior and use of sites with corresponding changes in the availability of certain aquatic habitats, and distribution and abundance of prey. Feeding behaviors observed for *T. cyrtopsis* in this study suggest that this snake forages as a generalist. Snakes fed almost exclusively near, on, or immediately below the water surface; no active midwater-diving or bottom-crawling, behaviors employed by aquatic specialists, were used by *T. cyrtopsis* to capture prey. However, *T. cyrtopsis* has evolved behaviors that appear to enhance the use of seasonally variable, aquatic resources. These behaviors may explain how this snake has been able to thrive in highly variable, aquatic habitats within desert regions. In terms of distribution in the desert Southwest, *T. cyrtopsis* is an aquatic habitat specialist.

Certain species of garter snakes (*Thamnophis*) and water snakes (*Nerodia*) have specific behavioral and physiological characteristics that facilitate feeding on aquatic organisms, including bottom-crawling and negative buoyancy (Drummond, 1983). Drummond (1983) divided snakes in the genera *Thamnophis* and *Nerodia* into two categories: snakes that forage as specialists and snakes that forage as generalists. Aquatic-foraging specialists possess physical and behavioral characteristics that enable them to feed on aquatic organisms within several different water columns in a stream or lake. These aquatic specialists feed almost exclusively on aquatic organisms. Conversely, aquatic-foraging generalists lack these physical and behavioral characteristics and are, therefore, unable to feed upon aquatic organisms within various water columns. These snakes feed on a wide variety of prey, including semi-aquatic and terrestrial organisms (Drummond 1983). Additionally, since larger snakes should be able to maintain activity for longer periods of time than smaller snakes (see Pough, 1977) and since larger snakes can eat both large and small prey (Mushinsky et al., 1982), there may be differ-

ences in feeding behavior and habitat use among different-sized garter snakes of the same species.

Although Patterson and Davies (1982) and Arnold and Wassersug (1978) observed predatory behavior in *Natrix* and *Thamnophis*, respectively, observations of this behavior in free-roaming snakes are rare. *Thamnophis cyrtopsis*, the black-necked garter snake, a locally abundant snake restricted to riparian corridors in many parts of the southwestern United States, presents an excellent opportunity to observe habitat uses and predatory behavior in the field. Such desert southwestern riparian and aquatic habitats are dynamic, with seasonal and yearly fluctuations in main-channel stream location, water level, and structure (Minckley, 1973; Minckley and Brown, 1982). Although terrestrial habitat structure (e.g., vegetation) is relatively stable within and between years, the relative amount and size of aquatic habitats (e.g., pools) along riparian corridors vary both seasonally and yearly, mostly in response to precipitation on the watershed. Because of these fluctuations, frogs, toads, tadpoles, and fish, common food items of *T. cyrtopsis* (Fleaharty, 1967), should be relatively uncrowded and widely dis-

persed during the spring and highly concentrated and unevenly dispersed in the summer. I studied *T. cyrtopsis* along two creeks in west-central Arizona to determine how seasonal changes in aquatic habitats affect the distribution and availability of potential prey of *T. cyrtopsis*, how seasonal changes in aquatic habitats affect the distribution of *T. cyrtopsis*, if these snakes forage as generalists, as suggested by Drummond (1983), if they vary their predatory behavior with changes in aquatic habitats and prey availability, if different-sized snakes use different habitats and predatory behaviors, and if other ecological factors such as reproduction, in addition to prey availability, contribute to the use of certain aquatic habitats by *T. cyrtopsis*.

MATERIALS AND METHODS—Two populations of *T. cyrtopsis* were studied, one along Burro Creek and one along Francis Creek, 13 km west and 23 km northwest of Bagdad, Mohave Co., Arizona, respectively. The site at Burro Creek was a broad (>200 m), low-gradient floodplain of cottonwood (*Populus fremontii*), Goodding willow (*Salix gooddingii*), mesquite (*Prosopis velutina*), and seep willow (*Baccharis*). Aquatic habitats were mostly runs, riffles, and associated backwaters between March and May and shallow and deep landlocked, backwater pools between June and October. Large exposed cottonwood and willow roots occurred along backwater pool banks, and these pools became covered with algae during low discharge.

The site at Francis Creek was a narrow floodplain (<75 m wide) dominated by mostly riffles and runs between February and May. Between June and October, aquatic habitats were mostly small, rock-bound pools formed by large boulders in slow-moving riffles, and deep landlocked pools. Algae also covered these pools during low discharge and exposed tree roots were common along pool banks. Dominant vegetation included cottonwood, Arizona sycamore (*Platanus wrightii*), velvet ash (*Fraxinus pennsylvanicus*), Arizona alder (*Alnus oblongifolia*), Arizona walnut (*Juglans major*), and seep willow. Stream discharge data for 1981 through 1983 were obtained from the U.S. Geological Survey's instream flow station no. 94224447 located on Burro Creek near Bagdad, Arizona.

Snakes were located by walking through riparian and aquatic habitats between 0600 and 2000 h each month (total of 48 transects; 12 in 1978, 1981, 1982, and 1983) in September to October 1978, March to August 1981, May to August 1982, and March to October 1983. Each walking transect was 500 m long. Habitats traversed by transects typically included riffles, runs, backwater pools, and areas adjacent to aquatic habitats, such as boulder piles, exposed tree roots, and gravel and bareground substrates, although some

of these habitats (e.g., riffles) were uncommon along transects walked between June and October. Aquatic habitat abundance was calculated as the number of each aquatic habitat encountered per 500-m transect. Each snake encountered along transects was examined to determine its sex, measured (snout-vent length, SVL), uniquely scale-clipped, and then released at the site of capture. Snakes were classified into three size classes based on SVL: adults (>25 cm), subadults and juveniles (11 to 25 cm), and newborns (<10 cm). Snake abundance was calculated for each aquatic habitat as the number of snakes seen per 10 m (total of 48; 500-m transects).

Behavioral observations of snakes encountered along transects were usually made at distances of >3 m. Individual snakes were followed and observed for as long as possible (e.g., until the snake retreated into cover), and the average observation time/snake was 3.4 h (range of 0.5 to 10.1 h; total of 93 observation periods). The time spent making behavioral observations was separated from the time spent walking transects. Use of various habitats by snakes was recorded with behavioral observations such as feeding postures, pursuit and capture of prey, types of movement, parturition, and escape. Behavior and habitat use were also compiled for snakes when initially located on transects. Diets of *T. cyrtopsis* were determined by forced regurgitation (method as described by Carpenter, 1952).

The abundance of *Rana yavapaiensis*, *Hyla arenicolor*, *Bufo punctatus*, *Bufo microscaphus* × *Bufo woodhousei*, and tadpoles of these species was determined by counting the number of individuals of each species in each aquatic habitat (number/100 m² of habitat) while looking for snakes and during separate searches conducted at night (73 total searches). Only very general observations of fish abundance were noted in each aquatic habitat, and identification of certain fishes in different aquatic habitats was inferred from Kepner (1980).

RESULTS—The abundance of aquatic habitats varied between spring (March to May) and summer (June to October) and was correlated with mean daily discharge (Table 1). Mean discharge between 1981 and 1983 was higher in spring ($\bar{X} = 206.46 \pm 1,167$) than in summer (1.84 ± 7.51), but these differences were not significant because of variability within years ($P > 0.05$). However, riffle and run abundance were positively correlated with discharge, and pool abundance was negatively correlated with discharge (Table 1). Riffles and runs were significantly more abundant in spring, whereas large and small pools were greater in summer.

The abundance of *T. cyrtopsis* in aquatic habitats also shifted between seasons. *Thamnophis cyrtopsis* was evenly distributed among aquatic

TABLE 1—Abundance of aquatic habitats in spring versus summer. Mean abundance is the number of each aquatic habitat per 500-m transect ± 1 SD (total of 48 transects). Differences between spring and summer were significant ($P < 0.05$; Student's *t*-test) for each aquatic habitat. Abundance of individual aquatic habitats was a function of discharge (significant at $P < 0.05$ for each aquatic habitat).

Aquatic habitat	Spring	Summer	Relation-ship to discharge (r^2)
Riffles (>10 m)	12.1 \pm 3.4	1.6 \pm 1.1	0.89
Runs (>10 m)	19.6 \pm 4.1	6.5 \pm 2.8	0.83
Pools (>100 m ²)	5.8 \pm 2.3	17.6 \pm 4.5	-0.76

habitats in spring ($\chi^2 = 0.41$; not significant at $P < 0.05$) and unevenly distributed in pools during summer ($\chi^2 = 8.94$; significant at $P < 0.05$; Table 2). The abundance of *T. cyrtopsis* in summer in pools was also significantly greater than in spring (Table 2). A similar shift was also observed for potential prey of *T. cyrtopsis*, although prey were unevenly distributed in pools and runs during spring (Table 3). Snake abundance in aquatic habitats, when submitted to a step-wise multiple regression analysis, was largely explained by total prey abundance (82% of the regression variability reduced; $P < 0.05$) and to a lesser degree by the abundance of *R. yavapaiensis* (9% of the regression variability reduced; $P < 0.05$), *H. arenicolor* (3% of the regression variability reduced; $P < 0.05$), and tadpoles (3% of the regression variability reduced; $P < 0.05$). The clustered distribution of adult *R. yavapaiensis* and tadpoles in pools during summer reflect the scarcity of other aquatic habitats during these low flow periods.

Adult and subadult *T. cyrtopsis* were first observed moving along streambanks during spring, and four adults were also observed during this period at least 0.5 km from aquatic habitat in adjacent desert. Snakes used a variety of overnight cover sites, such as exposed roots along streambanks, rodent holes in adjacent desert, crevices in streambanks and rock, and vegetative debris piles created by high discharge.

During summer, snakes were observed near or in pools, few being observed along slow-moving runs and riffles (Fig. 1). Adults used exposed tree

TABLE 2—Abundance of *Thamnophis cyrtopsis* in aquatic habitats. Mean abundance is the number of snakes seen per 10 m along transects ± 1 SD (total of 48 transects).

Aquatic habitat ¹	Spring ²	Summer ³
Riffles	1.7 \pm 1.1	0.9 \pm 0.6
Runs	3.1 \pm 2.0	1.5 \pm 1.3
Pools	2.6 \pm 2.1	8.0 \pm 2.3

¹ Significant difference ($P < 0.05$; Student's *t*-test) between seasons only in pool habitat.

² No significant difference among aquatic habitats ($\chi^2 = 0.41$, $P \geq 0.05$).

³ Significant difference among aquatic habitats ($\chi^2 = 8.94$; $P < 0.05$).

roots for overnight retreats, subadults used exposed tree roots and rock and streambank crevices, and newborn snakes used rock and streambank crevices next to shallow landlocked pools near where they were born. Adults and subadults used primarily an active searching behavior to subdue prey during spring and a sit-and-wait (ambush) behavior during summer. Snakes moved more frequently during spring than summer, and they also spent more time basking during spring (Fig. 2). During spring, snakes moved along streambanks where they preyed upon individual adult *R. yavapaiensis* that occurred in clusters of up to 75 adult frogs; some frogs were on top of each other. Frogs remained inactive in clusters for up to 5 h, primarily between 0700 and 1000 h. Snakes also preyed upon adult *H. arenicolor* in areas dominated by boulders, particularly on Francis Creek. During summer, adult and subadult snakes were observed most frequently in a floating, semi-submerged posture (Figs. 1 and 2), camouflaged in algae mats on large pools (>100 m²). Adult *R. yavapaiensis* and *H. arenicolor* were captured when they swam by motionless, semi-submerged snakes. When a snake failed to grasp a frog on its initial attack, it usually pursued its prey for at least 1 m. This pursuit involved swimming on the water's surface and short duration (<10 s) dives. Only one of 13 frogs were captured after the initial strike failed. Except for successful attacks on frogs on terrestrial substrate, all observations of adult and subadult predation during summer were in water (snakes were successful in capturing 17 frogs in 29 feeding bouts).

A regression analysis on the proportion of a

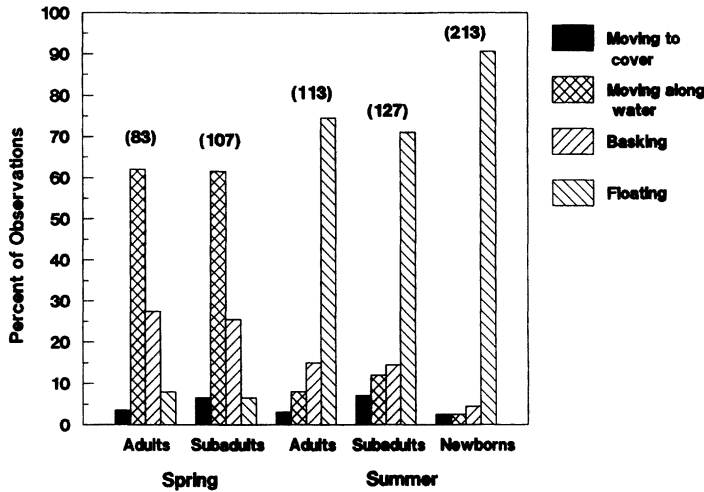


FIG. 1.—Frequency of behaviors of *Thamnophis cyrtopsis* when first encountered along walking transects. Numbers in parentheses = number of observations.

prey item in the diet of *T. cyrtopsis* (dependent variable, data from Fig. 3) and the relative abundance of that prey item (independent variable) showed a significant positive relationship ($P < 0.05$, $r^2 = 0.76$) between snake diets and prey abundance (both data sets arc-sin transformed for analysis). Generally, adult *T. cyrtopsis* consumed adult anurans that were most abundant. *Rana yavapaiensis* was the most abundant prey (Table 3) and the most common item in adult and subadult snake diets (Fig. 3). However, although *H.*

arenicolor was relatively common, this frog was a small proportion of the diet of *T. cyrtopsis* (Fig. 3). *Hyla arenicolor* was concealed in rock crevices along side rock-dominated pools during the day when *T. cyrtopsis* was active and, hence, was less vulnerable to predation. Conversely, *R. yavapaiensis* was more vulnerable to predation because it was poorly concealed and because it was concentrated in clusters. Therefore, vulnerability as well as prey abundance appear to influence the type and amount of prey eaten by *T. cyrtopsis*.

TABLE 3—Abundance of *Thamnophis cyrtopsis* prey in aquatic habitats in spring and summer. Mean abundance is the number of each species seen per 100 m² of each aquatic habitat (total of 73 searches). RAYA = *Rana yavapaiensis*, HYAR = *Hyla arenicolor*, BUPU = *Bufo punctatus*, Hybrid = *Bufo microscaphus* × *Bufo woodhousei* hybrid, and TP = tadpoles.

Aquatic habitat	RAYA	HYAR	BUPU	Hybrid	TP	Total abundance
Spring						
Riffles	4.3 ± 1.8 ¹	1.4 ± 1.1	5.9 ± 2.7 ¹	0.4 ± 0.2	2.1 ± 0.9	14.1 ± 2.6 ¹
Runs	9.4 ± 12.7	6.2 ± 4.0 ¹	1.3 ± 0.9	7.1 ± 4.5	30.8 ± 13.3	54.8 ± 16.9 ¹
Pools	5.3 ± 3.1	7.8 ± 3.7	5.1 ± 3.4	4.7 ± 3.0	37.5 ± 16.9	60.4 ± 12.9
χ ²	2.3	4.3	2.9	5.7	30.1 ²	29.6 ²
Summer						
Riffles	1.1 ± 0.7	3.1 ± 1.9	1.8 ± 1.5	0.5 ± 0.3	46.0 ± 17.2 ¹	8.5 ± 2.5
Runs	2.6 ± 1.4	0.1 ± 0.1	1.9 ± 1.2	8.2 ± 3.8	13.8 ± 5.6	26.6 ± 6.3
Pools	46.0 ± 17.2	8.3 ± 1.9	7.7 ± 2.9	6.5 ± 3.1	85.0 ± 9.7 ¹	153.5 ± 21.7 ¹
χ ²	78.5 ²	9.0 ²	6.0 ²	6.5 ²	120.2 ²	198.6 ²

¹ Significantly greater during spring than summer ($P < 0.05$; Student's *t*-test).

² Significant ($P < 0.05$) difference among aquatic habitats.

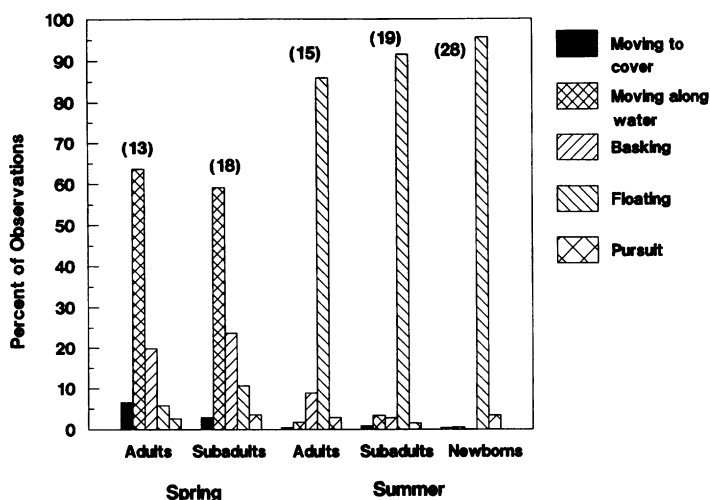


FIG. 2.—Frequency of behaviors of *Thamnophis cyrtopsis* observed during continuous observation periods. Numbers in parentheses = number of snakes observed performing the behavior.

Tadpoles approaching metamorphosis comprised the majority of total tadpoles consumed by adult and subadult snakes. Of 276 tadpoles from snake stomachs, 80% were transforming from the larval to adult stage. Although tadpole metamorphosis occurred throughout the study period, it was most common in July.

Four females were observed giving birth on 29 June, 11 July, 17 July, and 19 July, respectively. Litter sizes were 14, 19, 21, and 22, and the four females gave birth to young while partially sub-

merged in landlocked pools. Newborn garter snakes were observed most frequently floating in small (<10 m²) landlocked pools (Fig. 1) that were crowded with fish (several hundred) and tadpoles. Snakes remained motionless, floating semi-submerged in alga patches with their heads above the water's surface until a fish or tadpole moved. They then struck at the movement and attempted to capture the prey (successfully capturing prey on 24 of 59 attempts). On four occasions, newborn snakes were observed eating dead

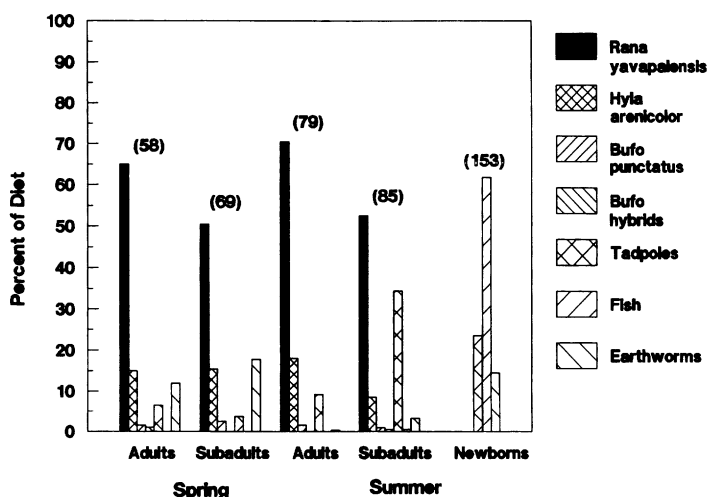


FIG. 3.—Percentage of prey types in diets of *Thamnophis cyrtopsis*. Numbers in parentheses = number of snakes with food in their stomachs.

fish in nearly dried pools. Prey were limited to small fish and tadpoles (including transforming tadpoles; Fig. 3).

DISCUSSION—Differences in habitat use by adult, subadult, and newborn garter snakes may result from selective pressures imposed by a number of interrelated ecological factors. The availability of aquatic habitats during different times of the year and the corresponding distribution of potential prey appear to be of primary importance in determining the distribution of *T. cyrtopsis*. In spring, prey were relatively widespread because aquatic habitats were abundant and diverse; there were a number of different aquatic habitats in which prey could be found. During summer, adult and subadult snakes shifted their habitat use from streambanks to landlocked and mainstream pools where adult and larval frogs and toads were abundant. Other habitats, such as runs and riffles, were scarce during summer. Prey available to *T. cyrtopsis* at different times of the year is, therefore, a function of the amount and distribution of certain aquatic habitats, which is a function of discharge. Fouquette (1954) suggested that *T. cyrtopsis* is an opportunistic forager, moving to areas where prey are most abundant.

Several other factors, such as locating mates for reproduction and thermoregulation, may, in part, be responsible for movements during the spring. Presumably, the probability of male-female interactions is increased by movement between and to these widely dispersed, food-rich areas. Additionally, ambient temperatures in spring may be more suitable for movement than in summer; daytime temperatures in summer often exceed 40°C.

In addition to prey distribution, the types and range of species eaten by *T. cyrtopsis* on Burro and Francis creeks also appears to reflect prey abundance and vulnerability. Generally, the proportion of prey items in the diet of *T. cyrtopsis* reflects the abundance of prey in the habitat occupied by individual snakes. However, prey vulnerability also appears to influence prey selected by *T. cyrtopsis*. Adult and subadult snakes foraged on clustered *R. yavapaiensis* along exposed banks of pools and runs. Clustered prey should be easier to capture than individual frogs. Wendleken (1978) observed ribbon snake predation on *Acris* and found that these frogs were able to escape *Thamnophis proximus* by leaping away from approaching snakes (of 10 attempted captures, no

snakes were successful). Additionally, the high incidence of transforming tadpoles and fish in the diet of newborn *T. cyrtopsis* reflect the vulnerability of these prey. Transforming tadpoles are vulnerable because they can neither swim nor hop effectively enough to escape snakes (Arnold and Wassersug, 1978), and fish become vulnerable when they get trapped in small isolated pools during low flows (Patterson and Davies, 1982). However, during the spring, fish are abundant throughout aquatic habitats (Kepner, 1980), yet they make up a very small proportion of snake diets. Although fish are abundant they are difficult for snakes to capture.

The use of different predatory behavior in spring versus summer may reflect changes in the distribution and behavior of prey of *T. cyrtopsis*. Huey and Pianka (1981) suggest that the predation strategy used by reptiles reflects the behavior of potential prey. Widely foraging predation strategies are employed to locate prey that are sedentary whereas sit-and-wait strategies are used to obtain prey that move consistently. *Thamnophis cyrtopsis* used a widely foraging predatory behavior in spring to capture widely dispersed, relatively inactive prey and a sit-and-wait or ambush behavior in summer to capture actively moving tadpoles and adult frogs that were confined largely to deep pools. Newborn garter snakes, without exception, used a sit-and-wait behavior to feed upon an extremely abundant fish prey base. Normally, these fish move over sandy runs within aquatic habitats (Kepner, 1980) but become trapped in algae-dominated pools when flows subside. Patterson and Davies (1982) observed similar predatory behavior in *Natrix maura*. This snake was inefficient in capturing fish in deep or flowing waters but frequently preyed upon fish that had been trapped in small, shallow pools. Live-birth of *T. cyrtopsis* at or in small pools provide newborn snakes with an immediate food source.

Physiological attributes may, in part, explain the ability of *T. cyrtopsis* to use a sit-and-wait predatory behavior consisting of various floating postures. Fleharty (1967) found that *T. cyrtopsis* has a lower specific gravity than either *Thamnophis elegans* or *Thamnophis rufipunctatus*, both highly aquatic species, and suggested that this attribute facilitated semi-submerged floating (55% of the observations in his study). Drummond (1983) suggested that the types of predatory behaviors employed by *Thamnophis* and *Nerodia*

reflected the degree of buoyancy of these snakes in water. He found that aquatic specialists could become negatively buoyant and employed a series of behaviors to capture prey while fully submerged in water, including bottom-crawling. Drummond (1983) hypothesized that negative buoyancy allows these aquatic specialists to remain submerged in search and pursuit of prey. Conversely, generalists were positively buoyant and were unable to forage efficiently while completely submerged in water. Lower specific gravity and an inability to become negatively buoyant may explain why *T. cyrtopsis* does not employ extended feeding bouts while submerged under water and why fish are rare in adult snake diets. Drummond (1983) also suggested that specialists might possess a modified eye lens that enhances vision and detection of prey under water, whereas this feature may be absent in generalists such as *T. cyrtopsis*.

Differences in predatory behaviors employed by adult versus newborn snakes may reflect the amounts of oxygen in the blood of different-sized snakes. Pough (1977) found that newborn *Thamnophis sirtalis* could maintain activity for only 3 to 5 min before becoming exhausted, whereas adult snakes could remain active for 20 to 25 min. He hypothesized that low amounts of blood oxygen might limit small garter snakes to certain microhabitats, predation strategies, and prey size. Newborn snakes on Burro and Francis creeks employed only a highly sedentary predatory behavior to feed upon an extremely concentrated and vulnerable food resource. Lower amounts of blood oxygen may, in part, account for these observations. Additionally, differences in the size of prey taken by adult versus newborn snakes probably reflects physical limitations associated with size (see Mushinsky et al., 1982). Physically, adult snakes are capable of feeding upon prey ranging in size from small minnows to adult frogs, whereas newborn snakes are limited to smaller prey such as small minnows and tadpoles.

Competition with other snakes for aquatic resources does not appear to restrict *T. cyrtopsis* to certain aquatic habitats. Although several other species of snakes occur within the study area (see Jones, 1981), most are only facultative users of aquatic resources. More importantly, there are no other aquatic or semi-aquatic *Thamnophis* or *Nerodia* on either drainage.

Based on feeding behavior observed in this study, *T. cyrtopsis* is a predatory generalist, as

suggested but not confirmed by Drummond (1983). Snakes fed exclusively at or near the water's surface or on banks of pools and runs. In addition, floating was the most common aquatic posture observed; no snakes were observed performing deep aquatic dives or bottom-crawling (feeding behaviors commonly observed in aquatic specialists). Although a few snakes were observed diving, this behavior was probably associated with escape rather than active foraging.

Although *T. cyrtopsis* is, by Drummond's (1983) definition, a generalist, these snakes are mostly restricted to consistent water sources within the desert Southwest, as are many other species of *Thamnophis* (see Stebbins, 1985). This high degree of dependency on water is exemplified by Hensley's (1950) survey. He documented a relict population of *T. cyrtopsis* at a permanently watered, natural catchment in Organ Pipe National Monument; this species occurred nowhere else within the Ajo Mountains. In addition, as demonstrated in this study, *T. cyrtopsis* has apparently evolved behaviors that allow it to exploit seasonally variable, aquatic resources. Although this snake is a predatory generalist, it must be considered an aquatic habitat specialist within the desert Southwest.

I am indebted to H. K. McGinty, M. J. Fouquette, Jr., and S. Rissing for critical review of an earlier draft of this manuscript. I am also grateful to K. Relyea for additional observations of *T. cyrtopsis* along Burro Creek and to the U.S. Environmental Protection Agency for time in preparing this manuscript. This study was part of a more comprehensive survey of reptiles and amphibians funded by the U.S. Bureau of Land Management in Arizona.

LITERATURE CITED

- ARNOLD, S. J., AND R. J. WASSERSUG. 1978. Differential predation on metamorphic anurans by garter snakes (*Thamnophis*): social behavior as a possible defense. *Ecology*, 59:1014-1022.
- CARPENTER, C. C. 1952. Comparative ecology of the common garter snake (*Thamnophis s. sirtalis*), the ribbon snake (*Thamnophis s. sauritus*) and Butler's garter snake (*Thamnophis butleri*) in mixed populations. *Ecol. Monogr.*, 22:235-258.
- DRUMMOND, H. 1983. Aquatic foraging in garter snakes: a comparison of specialists and generalists. *Anim. Behav.*, 86:1-30.
- FLEHARTY, E. D. 1967. Comparative ecology of *Thamnophis elegans*, *T. cyrtopsis*, and *T. rufipunctatus* in New Mexico. *Southwest. Nat.*, 12:207-229.

- FOUQUETTE, M. J., JR. 1954. Food competition among four sympatric species of garter snakes, genus *Thamnophis*. *Texas J. Sci.*, 6:172-188.
- HENSLEY, M. M. 1950. Results of a herpetological reconnaissance in extreme southwestern Arizona and adjacent Sonora, with a description of a new species of the Sonoran whipsnake, *Masticophis bilineatus*. *Trans. Kansas Acad. Sci.*, 53:270-289.
- HUEY, R. B., AND E. R. PLANKA. 1981. Ecological consequences of foraging mode. *Ecology*, 62:991-999.
- JONES, K. B. 1981. Distribution, ecology, and habitat management of the reptiles and amphibians of the Hualapai-Aquarius Planning Area, Mohave and Yavapai counties, Arizona. Tech. Note, U.S. Bureau Land Mgmt., 353:1-137.
- KEPNER, W. G. 1980. Aquatic inventory of the upper Bill Williams drainage, Yavapai and Mohave counties, Arizona. Tech. Note, U.S. Bureau Land Mgmt., 352:1-57.
- MINCKLEY, W. L. 1973. Fishes of Arizona. Arizona Game Fish Dept., Phoenix, 293 pp.
- MINCKLEY, W. L., AND D. E. BROWN. 1982. Wetlands. Pp. 223-286, in *Desert plants* (D. E. Brown, ed.). Univ. Arizona Press, Tucson, 342 pp.
- MUSHINSKY, H. R., J. J. HEBBARD, AND D. S. VODOPICH. 1982. Ontogeny of water snake foraging ecology. *Ecology*, 63:1624-1629.
- PATTERSON, J. W., AND P. M. C. DAVIES. 1982. Predatory behavior and temperature relations in the snake *Natrix maura*. *Copeia*, 1982:472-474.
- POUGH, F. H. 1977. Ontogenetic change in blood oxygen capacity and maximum activity in garter snakes, *Thamnophis sirtalis*. *J. Comp. Physiol.*, 116:337-345.
- STEBBINS, R. C. 1985. A field guide to western reptiles and amphibians. Second ed. Houghton Mifflin Company, Boston, 279 pp.
- WENDELKEN, P. W. 1978. On prey-specific hunting behavior in the western ribbon snake, *Thamnophis proximus* (Reptilia, Serpentes, Colubridae). *J. Herpetol.*, 12:577-578.