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## DIFFERENTIAL PREDATION ON METAMORPHIC ANURANS BY GARTER SNAKES (*THAMNOPHIS*): SOCIAL BEHAVIOR AS A POSSIBLE DEFENSE<sup>1</sup>

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**Abstract.** The diets of garter snakes (*Thamnophis*) collected at several localities were examined and the developmental stage of anurans in the diets were recorded. During periods of anuran metamorphosis, garter snakes converge on the shoreline and their diets are biased towards transforming stages. This bias appears to reflect the locomotor ineptitude of metamorphosing anurans; transforming anurans can neither swim nor hop as effectively as premetamorphic tadpoles or postmetamorphic frogs, respectively.

Metamorphic synchrony in certain anurans (e.g., *Bufo*) may have evolved as a defense against predation during metamorphosis. This synchrony could satiate predators. Certain anurans (e.g., *Bufo*, *Scaphiopus*) form postmetamorphic aggregations which may represent 'selfish herds' in which individuals gain protection by association with more vulnerable conspecifics.

**Key words:** anurans; *Bufo*; California; differential predation; *Hyla*; metamorphic aggregation; metamorphic synchrony; metamorphosis; Mexico; Nevada; *Scaphiopus*; *Serpentes*; *Thamnophis*; Washington.

### INTRODUCTION

"The Lake is mostly surrounded by huge rushes higher than a man, among which are scattered stones of lava. On these one often sees half a bushel or more of toads piled in heaps. Garter snakes are proportionately abundant; one may walk miles and see one every 10 ft. I never saw so many snakes."<sup>2</sup>

Many organisms have intrinsically vulnerable stages in their life cycles. At such stages the organism has little or no defense once it is encountered by a predator. Vulnerable stages are often necessary consequences of transitions in the life cycle. For example, arthropods are vulnerable to predation during pupation, at eclosion and during molts (Mook et al. 1960; Tinbergen 1960; King and Dawson 1972; Gordon 1974; Stein 1975; Reaka 1976) and mammals may be particularly susceptible to predation during the first days of neonatal life (Estes 1976). Once detected by a predator, the recently eclosed arthropod and the neonate mammal fall prey because of their inability to flee.

Predation during vulnerable stages may be mitigated by cryptic coloration and behavior, parental care, social behavior or rapid passage through the stage. Adaptations for concealment and parental care are fa-

miliar solutions to the problem of transitory vulnerability: arthropods hide during molts, the downy young of shore-nesting birds are cryptically colored, newts wrap leaves around their eggs and some birds distract predators from the nest. High predatory risk at particular stages may also lead to selection for accelerated development (Williams 1966). In addition, certain social phenomena may lessen predatory risk during vulnerable stages. Many organisms synchronize risky transitions with conspecifics. Molt synchrony in crustaceans (Reaka 1976), eclosion synchrony in periodical cicadas (Lloyd and Dybas 1966), birth synchrony in wildebeest and caribou (Estes 1976; Dauphiné and McClure 1974), synchronous departure from hatching sites in lizards (Burghardt et al. 1977) and synchronous seeding in bamboos and other plants (Janzen 1971, 1976) have been viewed as antipredator adaptations.

Metamorphosis has been considered a hazardous transition for anurans; in this paper we confirm this view and explore some of its ramifications. Anuran metamorphosis involves extensive morphological reorganization. This suggests that anurans must descend from a larval "adaptive peak" in order to climb another adaptive peak represented by the adult phenotype (de Jongh 1968). In particular, the locomotor ability of metamorphosing anurans is limited, and laboratory studies indicate that anurans are particularly susceptible to snake predation during the metamorphic transition (Wassersug and Sperry 1977).

<sup>1</sup> Manuscript received 9 May 1977; accepted 26 June 1978.

<sup>2</sup> Observations by E. D. Cope in 1879 at Klamath Lake, Oregon, USA (Osborn 1931:486–7). The observations refer to the toad *Bufo boreas* (Cope 1889:271), probably at the time of metamorphosis.

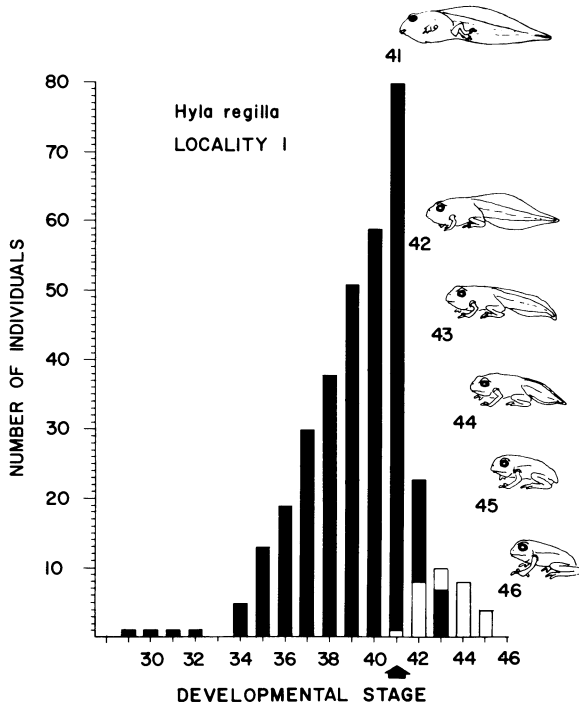


FIG. 1. The frequencies of anuran developmental stages in a pond sample and a *Thamnophis* stomach sample from locality 1 (0.5 km NNE of Colman Lake, Lassen County, California). Pond sample ( $n = 327$  anurans) is indicated with solid bars; stomach sample ( $n = 31$  anurans) is indicated with open bars. Bars indicating the 2 samples are superimposed (mode for stomach sample is stage 43). Arrows in this and subsequent figures indicate the last premetamorphic stage (41). Diagrams of anurans are after Volpe et al. (1961).

Metamorphosing or recently metamorphosed anurans have been noted in the diets of garter snakes (*Thamnophis*) by several authors (Fitch 1949, 1965; Fouquette 1954; Lagler and Salyer 1945; White and Kolb 1974; Licht 1974; and particularly Carpenter 1952). These studies do not allow us to assess the extent of differential predation on metamorphic stages because the precise developmental stages of ingested anurans were not reported. In this paper we present field evidence for vulnerability at metamorphosis for treefrogs (*Hyla*) and toads (*Bufo*).

Vulnerability to predation at metamorphosis may be a general feature of anuran life cycles. If this proves to be the case, then several aspects of anuran developmental biology can be viewed from a new perspective. We can, for example, seriously entertain the possibility that the rapidity of anuran metamorphosis is an adaptation to reduce predatory risk (Szarski 1957, Wassersug and Sperry 1977). In addition, the cryptic behavior of many anurans during metamorphosis and metamorphic synchrony in 2 genera (*Bufo* and *Scaphiopus*) may represent, in part, adaptations to avoid intense predation during metamorphosis.

## MATERIALS AND METHODS

Garter snakes (*Thamnophis elegans* and *Thamnophis sirtalis*) with anurans in their stomachs were captured at 5 localities in California, Washington and Mexico. A total of 359 anurans was recovered from 42 snakes. Samples of available prey were made at 2 of these localities. The developmental stages of anurans in these stomach and environmental samples were determined using a standard anuran developmental staging scheme (Gosner 1960). Stages 42–45, in which anurans have the forelimbs exposed but still retain part of the larval tail, designate metamorphosis (Fig. 1). All field samples and observations were made by the senior author; determinations of anuran developmental stages were done by the junior author.

Anurans were retrieved from snakes by forcing the snakes to regurgitate (Carpenter 1952). The sampled snake was held by the tail. By pressing its body between the thumb and index finger, the stomach contents were moved anterior to the esophagus. At this point the snakes usually began actively to regurgitate their ingested prey. The snakes were unharmed by the procedure, and some prey were still alive when regurgitated. Regurgitated prey from each snake were placed in separate perforated vials and preserved in 70% ethanol or 10% Formalin for subsequent identification. Body length for each snake was measured in the field by stretching the individual along a tape measure.

The anuran prey available to foraging snakes was sampled at 2 localities (1 and 5 below). Pond samples were made at both localities with a 3-m seine (3-mm mesh). The anurans captured in each seine haul were scooped into plastic bags and immediately placed on dry ice. Shore samples were taken at locality 5, where the anurans (*B. boreas*) formed terrestrial aggregations at the shoreline. Anurans in aggregations were herded into a small dip net, transferred to plastic bags and placed on dry ice. Shore and pond samples were kept frozen until analysis of developmental stages.

## STUDY LOCALITIES AND FIELD OBSERVATIONS

Locality 1 consisted of 2 small, temporary ponds and an adjoining moist meadow, 0.5 km NNE of Colman Lake, Lassen County, California, USA. At this site on 16 July 1975 we captured 5 *T. elegans* and 8 *T. sirtalis* with Pacific treefrogs (*Hyla regilla*,  $n = 31$ ) in their stomachs (Fig. 1). Only this prey had been eaten by the snakes. The snakes were found in and around a drying pond  $\approx 5$  m in diameter (6 cm deep) and around a second, larger pond 18 m  $\times$  7 m in diameter (50 cm deep). The 2 ponds were 240 m apart in a moist meadow. *Hyla regilla* larvae were abundant in both ponds. Due to the short distance between the ponds, the ingested anurans could have been captured in either pond. Consequently, the stomach samples from the snakes at the 2 ponds were pooled. A sample

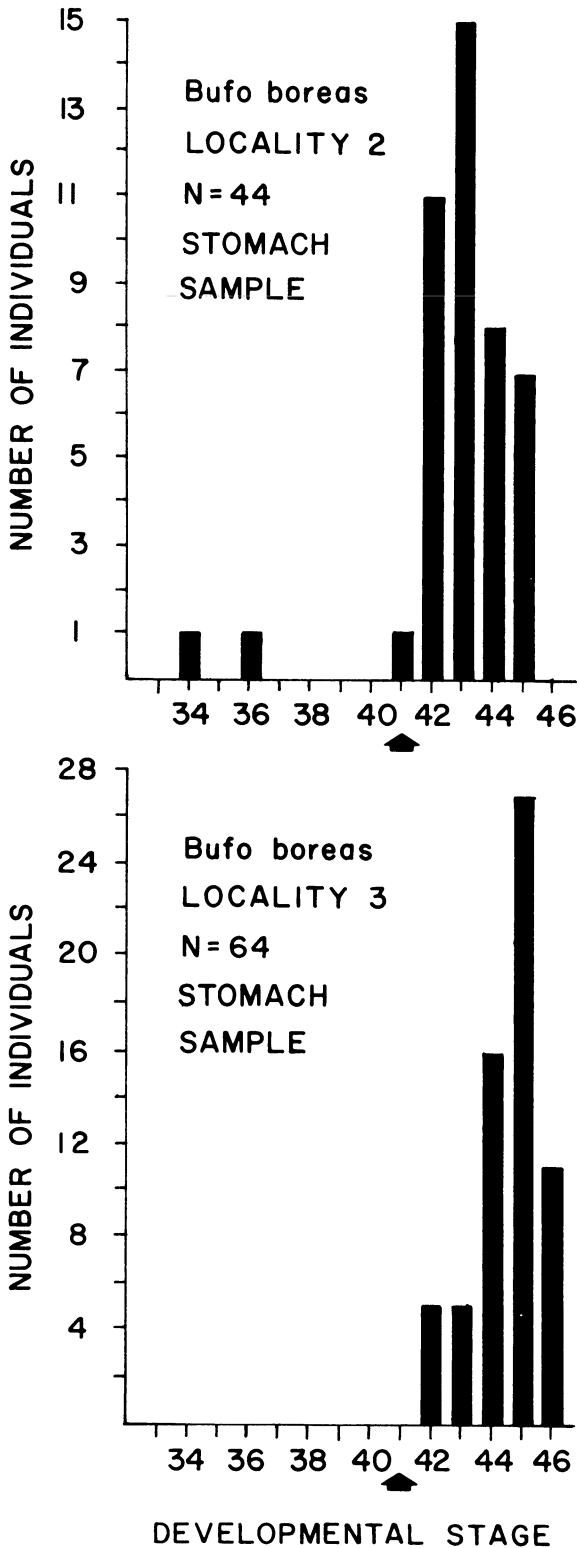


FIG. 2. Frequencies of anuran developmental stages in *Thamnophis* stomach samples from localities 2 (Colman Lake, Lassen County, California, above) and 3 (Eagle Lake, Lassen County, California, below). Sample sizes indicated in this and subsequent figures refer to numbers of anurans.

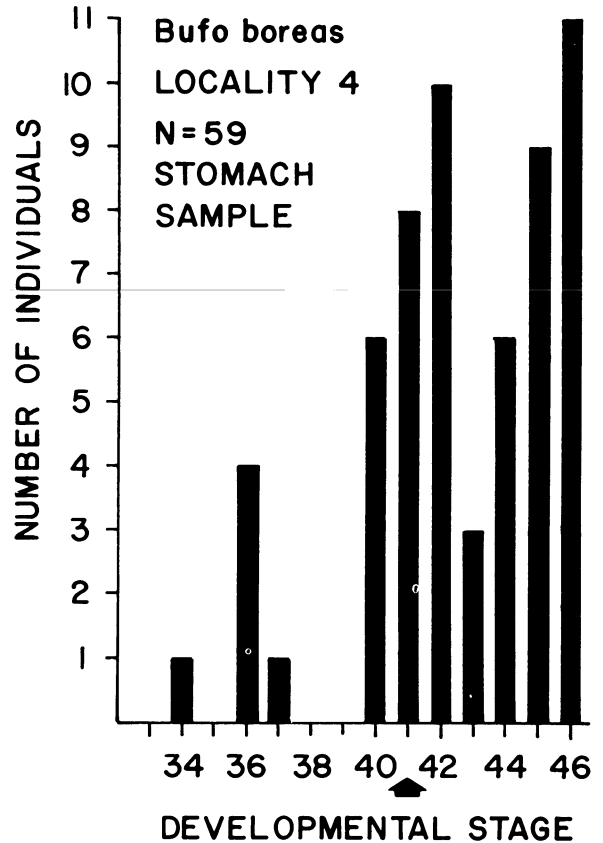


FIG. 3. Frequencies of anuran developmental stages in a *Thamnophis* stomach sample from locality 4 (Baja California Norte, Mexico).

of *H. regilla* ( $n = 327$ ) was taken by seine in the larger pond on 16 July 1975 (Fig. 1).

Locality 2 was Colman Lake, a small lake 7.2 km SE of the southern tip of Eagle Lake, Lassen County, California, USA. When this site was visited on 18 July 1975 *T. sirtalis* were abundant along the shore, but no *T. elegans* were observed. Seven *T. sirtalis* had Western Toads (*Bufo boreas*,  $n = 44$ ) in their stomachs (Fig. 2), but no other prey species were recovered from any of the snakes. Despite the prevalence of *B. boreas* in the snake stomachs, we failed to find metamorphosing toads along the shore or larvae in the water.

Locality 3, Pikes Point on the SE shore of Eagle Lake, Lassen County, California, USA, was visited during July in 4 successive yr (1974–1977). Samples of *Thamnophis* preying on *Bufo boreas* were obtained in 1975. Metamorphosing *B. boreas* were abundant along the shore on 17 July 1975. In contrast, only a few metamorphosing toads were found on the preceding 5 days. (Only a few larvae were observed in the water on any observation day, but they may have been hidden in aquatic vegetation which was dense along the shore.) Recently metamorphosed *B. boreas* ( $n = 111$ ) were found in the stomachs of 29 *T. elegans*. Stomach

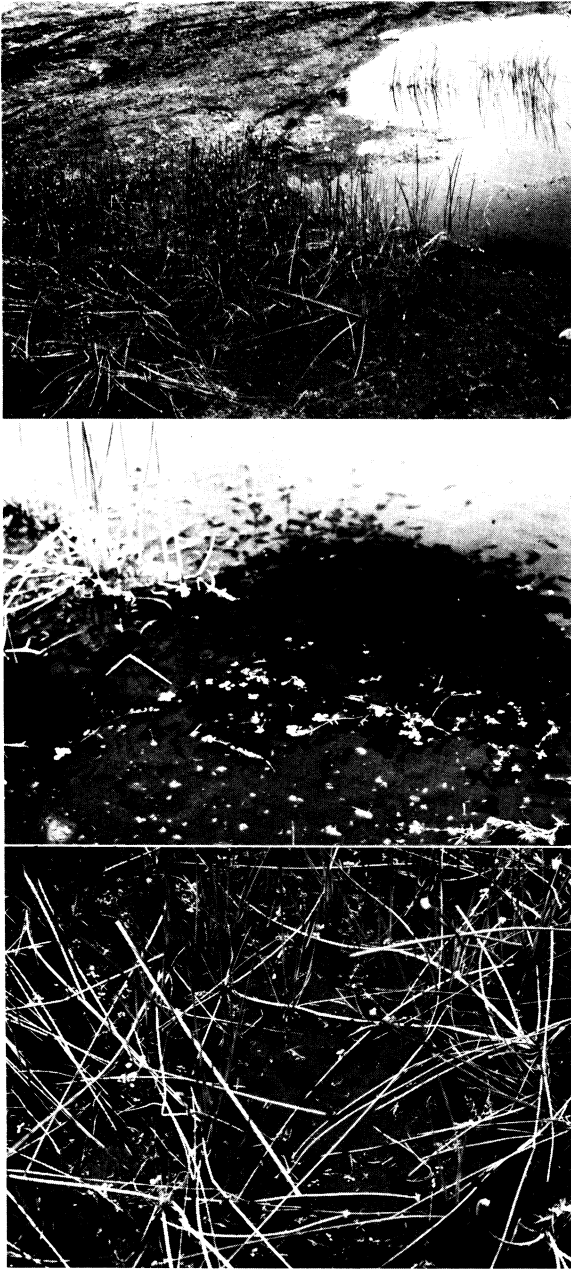


FIG. 4. A premetamorphic aggregation of larvae and an adjoining concentration of metamorphosing and metamorphosed *Bufo boreas* at locality 5B (Muck Creek, King County, Washington). (Upper) Habitat photograph showing an aquatic aggregation of premetamorphic larvae (lower right). A dense, terrestrial concentration of metamorphosing and metamorphosed toads occurred in the *Carex* stand (left and center). (Middle) Aquatic aggregation of larvae in closer view. (Lower) Terrestrial concentration of toads in closer view.

samples from 16 of these snakes were preserved and later staged (Fig. 2). *Bufo boreas* constituted 95% of the prey items in *T. elegans*, while fish (3 specimens) and leeches (3 specimens) constituted the remaining

fraction. One *T. sirtalis* with 12 metamorphosing *B. boreas* was also captured, but its stomach contents were not preserved.

Locality 4 was a moist meadow, La Grulla (Goldman 1951), adjoining a mountain stream in the Sierra San Pedro Matir, Baja California Norte, Mexico. When we visited this site on 31 May 1976, *B. boreas* larvae were extremely abundant in the stream. The larvae formed aggregations in small, quiet pools along the stream, and terrestrial aggregations of metamorphosing toads were found at intervals along the stream shore. *Hyla regilla* larvae were found in several small ponds not connected to the stream. Several adult *H. regilla* and a few *B. boreas* adults were found along the stream course. Only 2 garter snakes (*T. elegans*) were captured and only 1 of these (Fig. 3) had prey in its stomach (59 *B. boreas*). This individual was found in a shallow (4 cm deep) pool in the meadow adjoining the stream. The pool contained both *H. regilla* and *B. boreas* larvae but emergent vegetation thwarted sampling.

Locality 5, Muck Creek, 8 km ENE of Roy, King County, Washington, was visited on 13–14 June and on 22–23 June 1976. Two sites, 5A and 5B, 0.5 km apart along Muck Creek, were sampled for *B. boreas* and *Thamnophis*. The 2 sites consisted of ponds formed by overflow from Muck Creek. On 13–14 June, larval *B. boreas* were abundant at both sites 5A and 5B, but no metamorphosing or metamorphosed toads were present. Three *T. sirtalis* were captured with prey in their stomachs (2 fish, 2 *B. boreas* larvae and 2 *Rana catesbeiana* larvae). When the 2 sites were revisited on 22–23 June, metamorphosing as well as larval *B. boreas* were abundant. Larval *B. boreas* formed dense schools in shallow water at the pond margins (Fig. 4a and b). Recently metamorphosed toads were very abundant (10–50 toads/m<sup>2</sup>) for a distance of 0–3 m from the shoreline (Fig. 4c). Such concentrations of metamorphosed toads were found at intervals along the shoreline and each concentration covered an area of several m<sup>2</sup>. Terrestrial aggregations of metamorphosing and metamorphosed toads were found at the shoreline in some of these concentrations. Each aggregation was composed of 50 to a few hundred toads huddled together in a compact mass. In some instances, a dense school of larvae was present in the water immediately adjacent to a terrestrial aggregation of toads. No snakes were observed foraging in the water, but 6 *T. sirtalis* were captured on land amid concentrations of metamorphosing and metamorphosed toads. Two of these snakes, captured at site 5A on 22 June, had a total of 84 *B. boreas* in their stomachs (Fig. 5). Of the remaining 4 snakes, captured at site 5B on the same date, only 3 had identifiable stomach contents, and these yielded a total of 77 toads (Fig. 6). *Bufo boreas* were sampled at each site in the immediate vicinity of the snake captures. Two samples were taken at each site; a pond sample was taken in

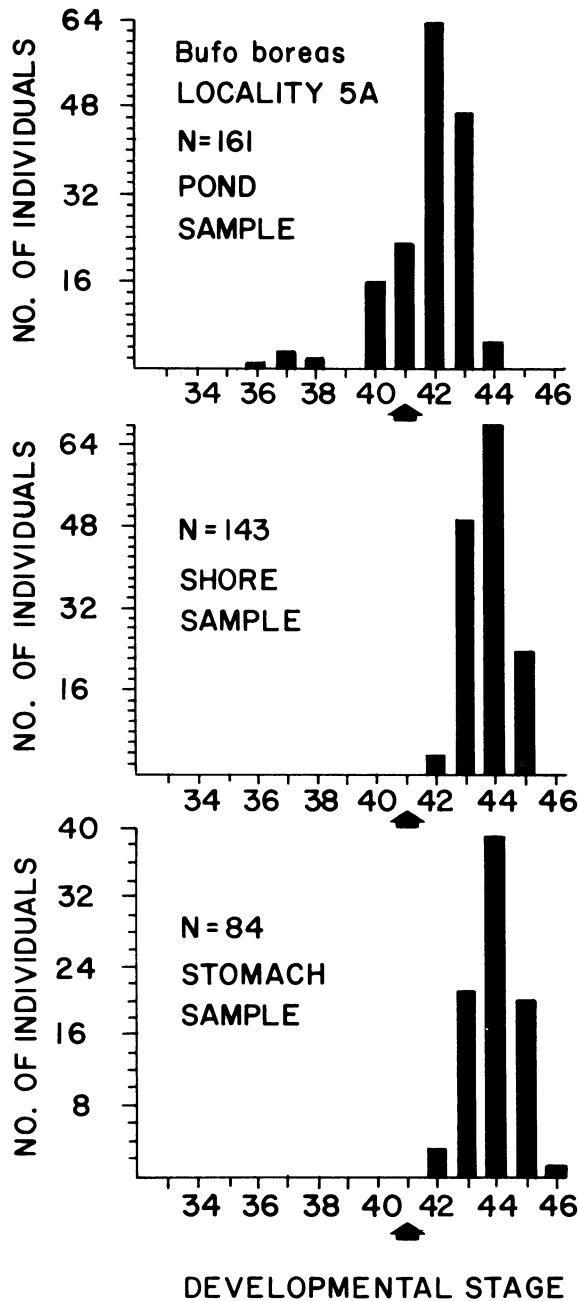


FIG. 5. Frequencies of anuran developmental stages in pond, shore and *Thamnophis* stomach samples from locality 5A (Muck Creek, King County, Washington).

the pond by seine, and a shore sample was taken on land adjacent to the shore with a dip net. The shore and pond samples were taken at site 5A on 22 June (Fig. 5) and at site 5B on 23 June (Fig. 6).

Observations on metamorphosing *Bufo*, the foraging behavior of *Thamnophis* and snake predation on *Bufo* larvae were made at several additional localities.

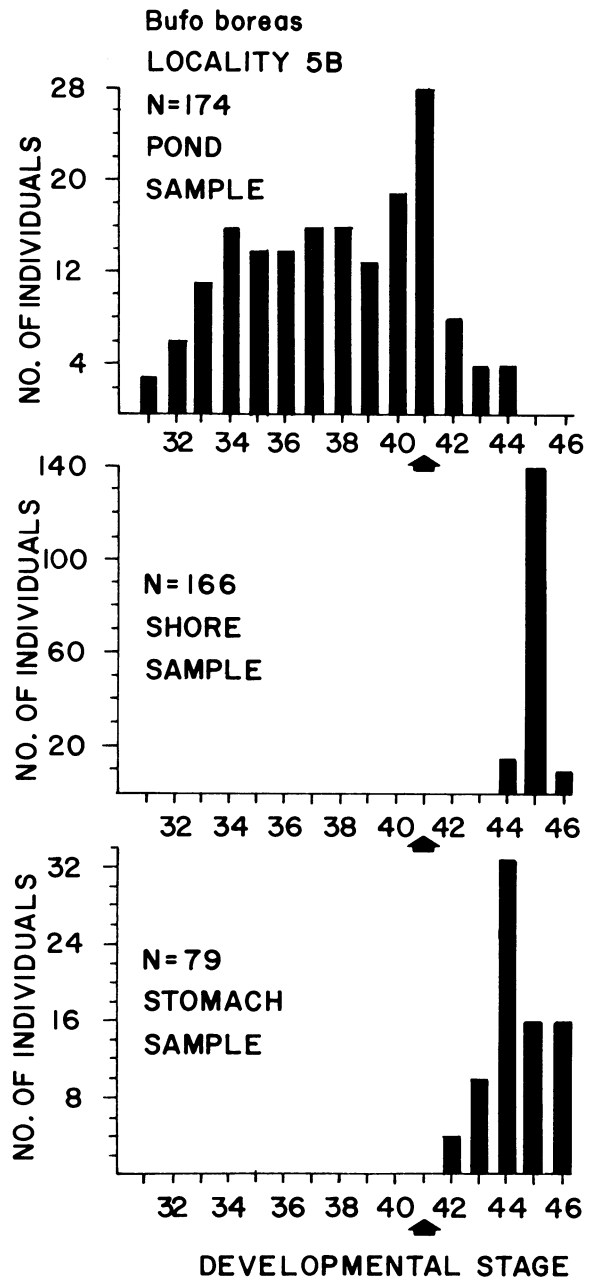


FIG. 6. Frequencies of anuran developmental stages in pond, shore and *Thamnophis* stomach samples from locality 5B (Muck Creek, King County, Washington).

The metamorphic and postmetamorphic behavior of *Bufo* was observed near Solvang, Santa Barbara County, California, USA, in May 1974 (*B. boreas*); near Ouarzazate, Morocco, on 2 January 1977 (*Bufo viridis*); near Concordia, Sinaloa, Mexico, on 19 May 1976 (*Bufo marinus*) and near Miraflores, Baja California Sur, Mexico, on 2 August 1975 (*Bufo punctatus*). At the last 2 localities we found a cat-eyed snake (*Lepidodeira maculata*) preying on transforming *B.*

*mazatlanensis* and water snakes (*Natrix valida*) preying on transforming *B. punctatus*. The aquatic foraging behavior of *T. elegans* and *T. sirtalis* was observed in Lassen and Sierra counties, California. Predation by snakes on premetamorphic *Bufo* was observed near Pacheco, Chihuahua, Mexico, on 8 May 1976 (*Thamnophis eques*); near Carmel, Monterey County, California, USA, on 5 July 1974 (*T. sirtalis*) and near Lemont, Cook County, Illinois, USA, in May 1975 (*Nerodia sipedon*).

#### RESULTS AND DISCUSSION

Transforming anurans (stages 42–45) predominated in all of the snake stomach samples (Fig. 1–6). Because this pattern of predation was observed at a variety of localities over a large geographic area (Mexico to Washington) and involved 2 morphologically different genera (*Bufo* and *Hyla*), we conclude that transforming anurans are generally susceptible to predation by *Thamnophis* and possibly other snakes. This is our main result.

We found snakes foraging along the shoreline, usually on land but sometimes in shallow water (1–4 cm), at all of our study localities. Metamorphic stages predominated in shoreline habitats (Figs. 5–6). Apparently, garter snakes actively converge on such habitats during periods of transformation. We observed dramatic changes in foraging site and diet when metamorphosing toads were available at locality 3. Transforming *Bufo* abounded at this locality in the summers of 1974 and 1975, but they were absent in the next 2 summers (these were drought years and apparently *Bufo* curtailed breeding even though habitats were not noticeably modified at the lake). In the first 2 yr transforming *Bufo* were abundant in shoreline meadows between rocky outcrops which protrude into the lake. Transforming *Bufo* were the dominant prey of snakes foraging in these meadows (Fig. 2). In contrast, garter snakes were virtually absent from these meadows in 1976 and 1977 when no transforming *Bufo* were present. Thus, garter snakes (*T. elegans*) shifted their foraging sites in years of anuran metamorphosis. In years with no metamorphosis the snakes foraged underwater next to the rocky outcrops and preyed on fish and leeches (a few snakes continued to forage in this habitat even when toads were transforming in the adjoining meadows in 1974–1975). We suspect that garter snakes commonly shift foraging sites in response to periods of anuran metamorphosis. How do snakes react to the spectrum of available developmental stages once they have converged on shoreline habitats in periods of metamorphosis?

Although garter snakes sometimes foraged in close proximity to schools of premetamorphic stages, they mainly captured transforming anurans in shoreline habitats. The relative absence of premetamorphic stages in the diet is particularly surprising because *T. elegans* and *T. sirtalis* will forage underwater in other

field contexts, and both species readily eat premetamorphic *Bufo* in captivity. At 3 localities (4, 5A and 5B) we observed premetamorphic stages massing in the water adjacent to shoreline concentrations of transforming anurans (Fig. 4). We observed garter snakes foraging on the shore adjacent to such schools of larvae at localities 5A and 5B, yet the snakes captured only metamorphic stages (Figs. 5–6). Thus, the relative absence of premetamorphic stages in the diet cannot be attributed to lack of opportunity. We suspect that the foraging sites and prey captures of these garter snakes are biased toward metamorphic stages because these stages are intrinsically vulnerable, specifically because they are inept at locomotion.

In the laboratory, transforming anurans are inferior to premetamorphic stages in swimming ability and inferior to postmetamorphic stages in jumping ability (Wassersug and Sperry 1977). The forelimbs of the transforming anuran appear to impede swimming and the tail interferes with jumping; the transforming anuran is neither a good larva nor a good frog. In laboratory trials, Wassersug and Sperry (1977) found that metamorphic anurans (*Pseudacris triseriata*) were less successful at evading capture by garter snakes than either premetamorphic or postpostmetamorphic stages. One of our field samples suggests that locomotor ability can affect predation in the field as well (Fig. 6). Although stage 44 predominated in stomach samples, this stage was uncommon both on the shore and in the pond. Of the 3 stages (44, 45, 46) present on the shore, stage 44 has the largest tail (Fig. 1) and probably the poorest jumping ability. This result tends to confirm expectations derived from laboratory experiments. However, it should be noted that the only other sample which permits a comparison of stomach and shore samples (Fig. 5) did not show differential predation among stages available on the shore. There, metamorphic stages predominated in the stomach samples, but they appeared to have been captured in proportion to their representation on the shore. Thus, within the shoreline habitats, captures were sometimes biased toward the most inept of available stages. These results, together with the general tendency of the snakes to forage where metamorphic stages abound, suggests that garter snakes in the field can exploit the locomotor ineptitude of metamorphic anurans.

The fact that transforming anurans suffer particularly intense predation has caused us to view transformation as an ecological hurdle. Transformation is clearly a problem for anurans regardless of what causes differential predation by snakes. Let us consider differential vulnerability at metamorphosis from the standpoint of the evolving anuran, in particular the propositions that anurans may be able to satiate predator populations by synchronizing metamorphosis and that individuals may also gain an advantage by aggregating with more vulnerable conspecifics.

Vulnerability to predation during metamorphosis

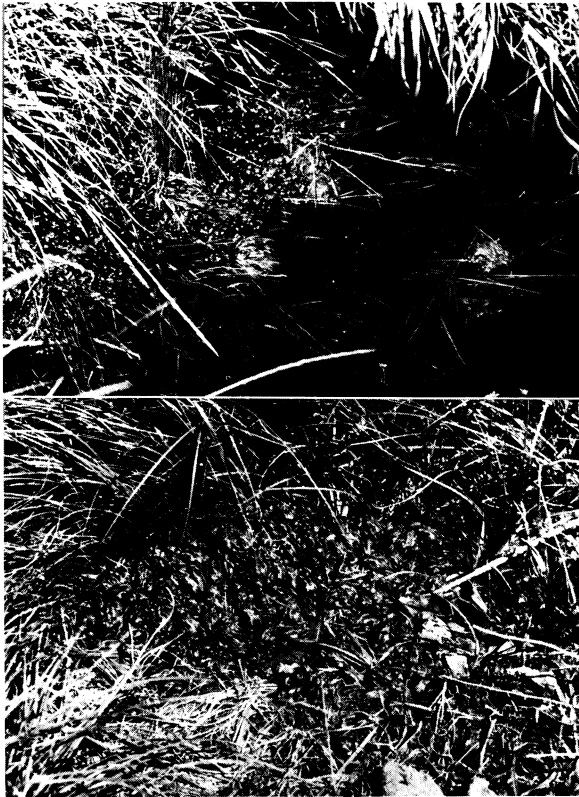


FIG. 7. Metamorphic and postmetamorphic aggregations of spadefoot toads (*Scaphiopus intermontanus*) near Elko, Nevada. (Top) Aggregation of metamorphic larvae on the edge of a temporary pond. (Bottom) Terrestrial aggregation of postmetamorphic spadefoots. At least 147 individuals are visible on the surface of the aggregation.

may explain some features of metamorphic behavior in the genus *Bufo*. These anurans are notable for the high densities they achieve during the metamorphic process and for their toxic qualities at all developmental stages. Toxins (indolealkylamines and polypeptides) probably protect *Bufo* species from many predators, particularly birds, fish and most mammals (Voris and Bacon 1966; Licht 1968; Licht and Low 1968; Heusser 1971; Cei et al. 1972; Low 1972; Cooke 1974). However, some predators (hedgehogs; leeches; odonate larvae; some predaceous anuran larvae; and many snake genera, including *Thamnophis*) are apparently immune to *Bufo* toxins (Fitch 1936, 1941, 1949; Uhler et al. 1939; Lagler and Salyer 1945; Tanner 1949; Hamilton 1951; Carpenter 1952; Fouquette 1954; Hanson and Vial 1956; Brockelman 1969; Heyer et al. 1975; Brodie 1977). Larval *Bufo* often move about in large schools (Beiswenger and Test 1966, Wassersug 1973). When metamorphosis occurs, small toads often congregate in large numbers on the margins of larval ponds. We observed high densities (10–50 toads/m<sup>2</sup>) of metamorphosing and metamorphosed *B. boreas* at 3 of our study sites (3, 4 and 5). We have observed

recently metamorphosed *Bufo viridis*, *B. punctatus*, and *B. marinus* at comparable densities. Bragg and Brooks (1958), Campbell (1934), Power (1926) and F. Breden (*personal communication*) report similar concentrations of metamorphosing *Bufo cognatus*, *Bufo carens*, *B. punctatus* and *Bufo marinus*; at least 1 ranid, *Ambystoma subsigillata*, whose larvae resemble those of *Bufo*, also exhibits this behavior (Knoepffler 1976).

Young *Bufo* probably reach high densities because metamorphosis is synchronized in local populations. Henry Wilbur (*personal communication*) found that *Bufo americanus* showed pronounced metamorphic synchrony (in contrast to sympatric *Rana palustris* and *Rana sylvatica*). Bragg (1952) reports the same phenomenon, as well as aquatic aggregation of metamorphic larvae, in *Bufo terrestris*. At 1 of our study sites (locality 3), the density of recently metamorphosed *B. boreas* increased by at least 2 orders of magnitude during a 24-h period. Afterwards, the lake shore swarmed with thousands of toads.

*Bufo* may protect themselves from predation by synchronizing metamorphosis and thereby satiating predator populations. Such a proposal is especially feasible for a toxic animal like *Bufo*, because their toxicity reduces the spectrum of potential predators. In addition, larval populations are often very large; tens of thousands of larval *Bufo* can often be seen in a single pond. When thousands of *Bufo* metamorphose at once, escape by predator satiation is a likely consequence. At least some of the snakes in our sample were gorged, and presumably satiated, with metamorphosing toads.

Metamorphosing toads may clump in space as well as in time. Metamorphosing *B. boreas* sometimes aggregate into compact groups of 50 to several hundred individuals in which the toads may be stacked 2–3 deep (Black and Black 1969, Lillywhite and Wassersug 1974). Such aggregations occurred at 2 of our study sites (4 and 5). Spatial aggregation may protect individuals from predation through safety in numbers, but in addition it may have a special advantage for toads in advanced stages of metamorphosis. When aggregations of *B. boreas* are approached by a human observer, the toads disperse immediately. Because aggregations are composed of toads in various stages of metamorphosis (Figs. 4 and 5), and hence locomotor ability, the younger stages may be more vulnerable to a predator that enters an aggregation. As the toads disperse out of the aggregate, the younger stages may fall behind and suffer predation. Thus *Bufo* aggregations may represent selfish herds (Hamilton 1971) in which individuals gain protection by association with more vulnerable conspecifics.

Some aspects of the larval and metamorphic biology of spadefoot toads (*Scaphiopus*) are similar to *Bufo*. Premetamorphic larvae often swim together in dense schools of a few thousand individuals (Bragg 1968,



Richmond 1947). The synchronous emergence of thousands of metamorphosing *Scaphiopus* has been observed on at least 2 occasions (Dickerson 1907; Bragg 1950). Bragg (1950) gave the following account for *Scaphiopus holbrooki*: "When first noted just after sunset, all tadpoles in the pool . . . were in two metamorphic aggregations near the shore-line. . . . The emergence of every tadpole in this mass took place within ten minutes. . . . Within fifteen minutes at the most, thousands of young spadefoots were on the bank and some were already hiding beneath objects near the shoreline and few if any tadpoles were left in the water. The next morning all had disappeared. A search of half an hour near the pool did not yield a single individual." Under some circumstances *Scaphiopus* do not immediately disperse after emergence. We observed postmetamorphic aggregations of *Scaphiopus intermontanus*, as well as premetamorphic schools and metamorphic aggregations, near Elko, Elko County, Nevada, USA on 27 June 1975. Large schools of larvae ( $\leq$ stage 41) swam about in a temporary pond at this locality. At several sites along the shoreline, metamorphosing larvae (stages 42–44) formed dense aggregations (Fig. 7a). Several piles of metamorphosed spadefoots ( $\geq$ stage 45) were also found, always a few to several metres from the nearest water (Fig. 7b). These piles were composed of a few hundred to several hundred individuals stacked 4–5 individuals deep at the center. The spadefoots in these piles slowly dispersed when approached. The toads at the surface of the piles were noticeably warmer than those lower in the piles (at midday). Surprisingly, we found slurries of dead, decomposing toads at the bottoms of the largest piles. Presumably these spadefoots were suffocated by the conspecifics above them. Some metamorphosed toads were not associated with the piles just described. Small groups, and even solitary individuals, were found under cover objects, and in some exposed places toads burrowed into the silty soil and formed a monolayer. We did not observe any potential predators other than birds. These birds,  $\approx$ 20 Snowy Egrets (*Leucophoyx thula*) and  $\approx$ 10 Black-crowned Night Herons (*Nycticorax nycticorax*), initially attracted us to the locality, and they may have been preying on this remarkable concentration of young spadefoots.

We suspect that metamorphic synchrony and metamorphic aggregation in *Bufo* (and perhaps *Scaphiopus*) are adaptations to reduce predatory risk, but we cannot refute other possibilities. The following possibilities, in particular, warrant investigation. (1) Metamorphic synchrony may represent mass exodus from a deteriorating larval environment. *Bufo* and *Scaphiopus* often breed in temporary ponds in xeric environments, and these ponds sometimes dry up before metamorphosis is completed (Richmond 1947; Bragg 1948). The appeal of this explanation is somewhat lessened by the observations that metamorphic synchrony

can occur in populations inhabiting permanent bodies of water (e.g., locality 3) and that it can occur before larval environments collapse due to evaporation (e.g., Elko, Nevada). (2) Metamorphic and postmetamorphic aggregation may reflect lack of opportunity, or inability, for long-distance dispersal. For example, terrestrial aggregations may be a fortuitous consequence of metamorphic synchrony occurring at times when weather conditions are unfavorable for dispersal away from the shoreline. The impressive size of *B. boreas* and *S. intermontanus* aggregations suggests, however, that they are formed actively rather than passively. (3) Aggregations may represent active protection against desiccation or insolation (Black and Black 1969). The thermal ecology of terrestrial aggregations in anurans has never been investigated. Our casual observations on *S. intermontanus* suggest that this may be an informative undertaking.

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