

INTRODUCTION

DRAFT

With few exceptions, North American anuran amphibians (toads and frogs) require free water for successful reproduction. Desert species, occupying areas where water is by definition scarce and often limiting, may be especially vulnerable to the redistribution of surface waters in the course of such activities as ranching, mining, agriculture and recreational development.

The object of this report is to provide land managers with basic data on five widespread species or species complexes of desert anurans (Scaphiopus intermontanus, Bufo punctatus, B. w. woodhousei/B. m. microscaphus, Hyla regilla, Hyla arenicolor) to assist informed management of breeding habitats. These data were derived from a BLM-supported study of anuran reproduction in northwestern Arizona and southeastern Utah during 1983, in conjunction with a review of relevant scientific literature. In addition, several key management topics are directly addressed in the concluding section of the report.

STUDY AREA: LOCATION, TOPOGRAPHY, AND RAINFALL

Study sites were located between $36^{\circ} 16'N$ and $37^{\circ} 02'N$, and $113^{\circ} 24'W$ and $114^{\circ} 02'W$, in extreme northwestern Arizona and southwestern Utah. The region is topographically complex, dominated by faulted mesas and benchlands and a minor mountain range, the Virgins. Elevations vary from approximately 500 meters near Lake Mead to approximately 2400 meters in the Virgin Mountains. The climate is arid, with 18.0 cm mean annual precipitation recorded at a site 572 meters in elevation (Beaver Dam, Arizona, $N = 20$ years); 22.3 cm at 841 meters (St. George, Utah, period of record = 1892-1975), and 27.1 cm at 1787 meters (Mount Trumbull, Arizona, $N = 43$

years)(Eubank & Brough, 1979; Brazel et al., 1981). Precipitation reaches a minimum at all elevations from mid-May to mid-July, and is otherwise fairly evenly distributed throughout the year.

DESCRIPTION OF STUDY SITES

Absolute and relative locations of the 11 sites monitored in this study are provided in Table 1 and Fig. 1.

Five sites (Grapevine, Ft. Pierce, Sand, Middle, Maple) comprised segments, 60-400 meters long, of relatively unmodified, spring-fed, perennial streams. Typical May, 1983 stream depths were 2-10 cm (Grapevine, Sand, Middle), 2-15 cm (Ft. Pierce), and 2-55 cm (Maple). Typical May, 1983 stream widths were 50-100 cm (Grapevine), 100-200 cm (Sand, Maple), and 100-300 cm (Ft. Pierce, Middle). All streams are bordered by sporadically dense shrubs, notably Pluchea sericea (Grapevine, Middle), Tamarix pentandra (Ft. Pierce, Sand), Robinia neomexicana (Maple), Baccharis glutinosa (Ft. Pierce, Middle), and Salix sp. (Maple). At Grapevine, significant shade is provided by an overstory of cottonwoods, Populus fremontii.

Six sites (Coyote, White Saddle, Cottonwood, Black Rock, Larson, Trail's End) are excavated cattle watering ponds, or "tanks". All sites were developed before 1965. Coyote, White Saddle, Cottonwood and Black Rock are spring-fed (water flows continuously through White Saddle and Black Rock tanks; Coyote and Cottonwood lack outflows), and perennial except for Cottonwood, which frequently dries for a short time in mid-summer (0-8 days in 1983). In addition, shallow, highly ephemeral tanks are found at Coyote and Black Rock. Larson and Trail's End are fed only by precipitation and runoff, but are both usually reliable water sources, and were perennial in 1983.

Approximate tank dimensions in May, 1983 were 0.9 x 8 x 10 m (Coyote), 0.5 x 4 x 20 m (White Saddle), 0.75 x 8 x 10 m (Cottonwood), 1 x 8 x 12 m (Black Rock, upper pool), 1.5 x 20 x 30 m (Larson), 2 x 30 x 45 m (Trail's End). Four tanks were partly shaded, by Baccharis glutinosa (White Saddle), Juniperus osteosperma (Black Rock), and Pinus ponderosa (Larson, Trail's End).

Metal, bathtub-sized stock troughs occur at three sites (Grapevine, Coyote, Cottonwood). Both Grapevine and Coyote were full throughout this study: water flowed continuously through the Coyote trough, and was regulated by a float valve at Grapevine. The level of Cottonwood varied considerably over the summer, with excess water periodically overflowing into Cottonwood tank.

METHODS

Biological and temperature data were collected at each site at approximately 10 day intervals (range = 8-14), over the period 7 April to 11 October. Anurans of all stages (eggs, larvae, juveniles, adults) found on the study sites were identified to species and counted at every visit. Prefeeding stages were classified according to Gosner (1960); older larvae were characterized as legless, having hind limbs/limb buds, or metamorphic. The body lengths of larvae (representative samples) and all juveniles/adults were measured to the nearest mm. Adult males were identified by throat characteristics and their tendency to vocalize (male release call) when gently squeezed behind the forelegs.

A representative sample of egg placement sites was described in terms of attachment substrate, depth of water, depth in water (if located in the

water column), distance from bank, relative water flow rate, and water temperature at eggs. Egg placement data for Scaphiopus intermontanus, Bufo w. woodhousei/B. m. microscaphus and Hyla arenicolor were collected both at study sites and less regularly visited locations. Temperatures at all sites were recorded with red alcohol field thermometers, calibrated in degrees C. Tadpole microhabitats were characterized in terms of range of water depths utilized, preferred feeding substrates, and associated water temperatures.

Livestock impact on study sites was monitored in terms of cropping of aquatic and semiaquatic plants, fecal contamination, and water turbidity. The relative abundance of potential tadpole predators (e.g. odonate naiads, notonectid adults and nymphs) was regularly recorded.

Water samples collected for chemical analyses were kept on ice until they could be tested or transferred to a refrigerator. All samples were analyzed within 36 hours of being collected. TDS (total dissolved solids) was assessed indirectly, using a Beckman SoluBridge conductance meter, at approximately 20 day intervals from early May through the end of September. Other tests were performed approximately at midmonth from May through September, using a Hach DR-EL portable chemical analysis kit. Tests methods were as follows: for orthophosphate levels, the Stannaver (stannous chloride) method; for nitrate/nitrite levels, the cadmium reduction (modified diazotization) method; for alkalinity, the phenolphthalein/brom cresol green-methyl red/sulfuric acid titration method.

Water temperatures varied within single tanks and streams as a function of depth, water flow, water volume, shading, season, and time of day. To minimize variability due to factors other than seasonal progression, temperatures were recorded at a single location and depth at each site: at midchannel in the main water flow at streams, and a depth of 8 cm, 35-40 cm

from the bank, at tanks. All temperatures were taken with a shaded field thermometer, in previously unshaded water. Diurnal variation was minimized by taking temperatures within 30 minutes of noon whenever possible. Alternatively, temperatures were taken as close to noon as possible, and extrapolated to 1200 hours based on the changes in temperature regularly noted between arrival and departure from a site.

RESULTS AND DISCUSSION

SCAPHIOPUS INTERMONTANUS

I. Distribution

Scaphiopus intermontanus is one of a closely related group of species including S. bombifrons, S. hammondi, and S. multiplicatus. Tanner (1939), Wright & Wright (1949), and Stebbins (1951) all considered S. intermontanus to be a subspecies of S. hammondi. As a group, these species occupy most of the United States west of Iowa and Missouri, and much of Mexico. S. intermontanus, the Great Basin spadefoot, occurs in Arizona north of the Colorado River, most of Utah and Nevada, southern Idaho, southwestern Wyoming, portions of western Colorado and New Mexico and eastern California, and eastern Oregon and Washington north to British Columbia (Stebbins, 1966).

II. Breeding Habitats

S. intermontanus bred at eight of the eleven study sites, ranging from 895 to 2145 m in elevation (Table 2). Stebbins (1966) states that this species has been found up to approximately 8500 feet (2600 meters). Both cattle tanks and spring-fed streams were readily utilized for breeding

purposes. Tadpoles were also found in roadside ditches that had been filled with rain a few days earlier (and were completely dry a few days later). The flexibility of this species in utilizing a diversity of water body types has been documented to extend to sewage, stagnant pools, swimming pools, and city reservoirs (Hardy, 1938), and the muddy water collected in cattle hoofprints (Stebbins, 1951).

Spadefoot tadpoles developed successfully over the full range of total dissolved solids, orthophosphate concentrations, and alkalinities recorded at sites in this study (Figs. 2,3). While spadefoots did not occur at Middle Spring, it seems unlikely (in view of this species' documented association with sewage) that this reflected the unusually high nitrate/nitrite concentrations at this site (Appendix 2). In fact, the only obvious common denominator of the three sites lacking S. intermontanus (Middle, Grapevine, White Saddle) is geographical: all are located in the Pakoon Basin, southeast of the Virgin Mountains. Spadefoot tadpoles were also not observed at apparently suitable ephemeral cattle tanks in this area (N = 5). The reason(s) for this absence, which is a real phenomenon at least at the study sites, is unclear. Pakoon waters are known to be utilized for breeding by three other anuran species, two of which (H. regilla, B. w. woodhousei) are undoubtedly less tolerant of xeric conditions than Scaphiopus species. In the case of White Saddle, a healthy spadefoot populations is established less than 6 km away, with no obvious major intervening barriers to dispersal, at Red Pockets Tanks. One possible explanation is that edaphic conditions around Pakoon waters are unsuitable for spadefoots: juveniles and adults of this group are highly fossorial, and Pakoon soils are notably thin, rocky, and underlain with hardpans (Bob Smith, BLM Arizona Strip District Hydrologist, pers. comm.). In southeastern Arizona, adult and juvenile S.

hammondii were invariably found buried in friable, sandy soil, although sometimes below a compacted surface layer (Ruibal et al., 1969).

As might be predicted, larval Scaphiopus are highly tolerant of anoxic waters. S. bombifrons tadpoles develop functional lungs no later, and possibly much earlier than Gosner stage 34 (i.e. having semi-developed hind legs)(Wassersug & Seibert, 1975) Black (1974) reports that the majority of a group of stage 30 S. bombifrons survived for 3 hours when evaporation stranded them on wet mud in the Oklahoma midafternoon sun; one tadpole minimally survived for nearly 20 hours.

III. Egg and Larval Microhabitats

Male S. intermontanus may call with only their hindquarters immersed at the edge of a pool (Stebbins, 1951), and mated individuals have been found along "a small trickle of water" running down a wash to a pond (Wood, 1935). In general, however, this species selects relatively deep water for breeding, ranging from 4 to 31 cm in this study (Table 3), and males call from a floating position. Eggs are attached in cylindrical masses to vertically-projecting objects such as dead twigs and live plant stems when these are available, from just below the water surface to about 20 cm in depth. In lieu of such supports, eggs are attached to bottom rocks and gravel, or even silt. Water flow rates in the relatively deep sections of stream favored by breeding spadefoots are typically slow.

Water temperatures at the depths at which S. intermontanus eggs occur are essentially those reported in Appendix 5. Egg masses may be warmer than the surrounding water on sunny days, especially in calm tanks and ponds. Zweifel (1965) found that a submerged mass of Rana pipiens eggs was as much as 2.4° C. warmer than the still water in a trough when both were exposed to

the sun for several hours; the difference was less given intermittent clouds or slow-flowing water.

S. intermontanus tadpoles are active swimmers, occurring throughout the water column. In streams, they will utilize areas of quite rapid flow (e.g. 15 cm/sec at the surface) if rocks or debris create pockets of quieter water where they can maintain a stable position while foraging. Tadpoles commonly feed at the water surface on fine, floating material; on filamentous algae floating on the surface or in the water column; on materials adhering to or growing on the surfaces of rocks; and on silty bottom sediments. Individuals tend to be fairly well dispersed, but may aggregate in response to patchily distributed food (e.g. locally thick clumps of algae). S. intermontanus tadpoles of all ages typically occur at 4 cm depth or (usually) more, but even very large individuals may occasionally be found foraging in 1-2 cm of water.

IV. Temporal Patterns

Breeding Patterns

Bragg (1965) characterizes Scaphiopus species as conforming to a xeric breeding pattern. Among the characters he cites as defining this pattern are: 1) occurrence of extended (opportunistic) breeding seasons, 2) very rapid larval development, and 3) the critical importance of rainfall as a proximate breeding stimulus. With certain reservations described below, these generalizations were found to apply to S. intermontanus

Table 4 lists the first and last dates when spadefoot eggs were deposited at study sites in 1983. Earliest oviposition dates appear to have been limited by temperature rather than precipitation, being markedly delayed with increasing elevation (range = 12 March at 895 m to 14 May at 2145 m).

Spring storms occur across wide fronts on the study area, and generally result in higher precipitation falling at higher elevations (rain gauge records, BLM Shivwits Resource Area, 1978-1983).

Adult activity and larval development in Scaphiopus are both limited by minimum threshold temperatures, although the exact values may vary with species and location. Bragg (1945) found that Oklahoma S. bombifrons rarely breed at air temperatures below 52° F. (11° C.), although males may call at 45° F. (7° C.). Surface emergence in S. couchi from the San Simon Valley (extreme southeastern Arizona and southwestern New Mexico) is inhibited by soil temperatures of 15° C. but not 20° C. (Dimmitt & Ruibal, 1980). Eggs of S. bombifrons and S. hammondi from this same area did not develop when held at temperatures below about 13° C.; S. hammondi eggs collected near Riverside, California developed at temperatures down to about 9° C. (Brown, 1966; Zweifel, 1968). Two possible instances of selection against early S. intermontanus reproduction occurring at unsuitably low water temperatures were observed in this study. On 3 May at Black Rock Tanks, 8 of a group of 64 egg masses were undeveloped and moldy, with the remaining embryos developed to Gosner stages 15-18. The water temperature at the eggs (located in full sun in a small pool not far from the spring source) was 15° C. at 1130 hours. On 17 May at Maple Spring, about half of a group of 19 egg masses were undeveloped and moldy, with the remaining embryos developed to Gosner stages 18-19. The water temperature at the eggs (located in 4-13 cm of slow flowing, shaded water) was 14.5° C. at 1200 hours. These were the only instances of moldy S. intermontanus eggs recorded in this study.

Precipitation often initiates breeding in S. intermontanus, but is not required for breeding to occur. At least five clutches of eggs were deposited over the course of this study when no rain had fallen in at least

the previous seven days. Linsdale (1938) reports that Nevada S. intermontanus bred in response to the flooding of pastureland (by diverted river water) without accompanying rainfall. It was probably the first such flooding to occur in at least three years. Similarly, Great Basin spadefoots were found in amplexus in a flooded field in Salt Lake County, Utah, where it had not rained for about three weeks (Stebbins, 1951).

Table 5 summarizes the temporal distribution of S. intermontanus clutches at study sites from March through August, 1983. While some females oviposited in all months, most reproduction at these reliable waters occurred from March to May. Peak reproduction in large populations tended to be fairly synchronous, occurring over periods of approximately 12 days (Ft. Pierce), 10 days (Sand), 8 days (Larson), and 10 days (Trail's End). The last clutches of the season were produced on approximately 3 and 18 August (Table 4). In eastern Oregon, Great Basin spadefoots have been reported to emerge (though not necessarily to breed) as late as October after heavy rains (Stebbins, 1951)

Several advantages may be derived from breeding early, where this is possible. Early metamorphosis allows the young maximum opportunities for same season growth. Relatively low evaporation rates increase the likelihood that tadpoles will have enough time to metamorphose from ephemeral tanks. At both permanent and less reliable sites, low mid-summer water levels may make tadpoles more susceptible to predation (see next section). High mid-summer water temperatures per se are more likely to help than hurt larvae, in that spadefoot tadpoles develop much faster at the upper than the lower limit of their viable temperature range (e.g. in the case of Arizona S. hammondi, almost 13 times faster to Gosner stage 20 (gill circulation) at 32.5° C. than at 13° C. (Brown, 1966)). Post-neurula embryos of S. hammondi are even

more heat tolerant than earlier stages, surviving temperatures as high as 39-40° C. (Brown, 1967). Cooling September water will, conversely, tend to slow larval development, and may make it difficult for late clutch larvae to successfully metamorphose before the advent of winter weather. Minimum transformation times in this study ranged from approximately 18 to 28 days, with some tadpoles taking two or more months to fully mature. By comparison, the minimum transformation time for Texas S. bombifrons tadpoles occupying an ephemeral ditch (mean water temperature = 29° C.), was found to be 15-20 days (Voss, 1961).

Adult and Juvenile Diurnal Occurrence

Metamorphosed spadefoot toads inhabit underground burrows for most of the year, and are primarily nocturnal when they emerge to feed and breed (Ruibal et al., 1969; Dimmitt & Ruibal, 1980). Juveniles, with greater energy requirements for growth than adults, are surface active for more days following rainfall (Creusere & Whitford, 1976), and may sometimes forage at midday (Linsdale, 1938). In the course of this study, adult spadefoots were observed diurnally on three occasions: a pair in amplexus at 1100 hours, 9 May (0% cloud cover; no recent rain) at Sand Spring; a single male at 1200 hours, 28 May (0% cloud cover; no recent rain) floating and calling briefly in Cottonwood Tank; a single male at 1300 hours, 2 July (30% cloud cover; no recent rain), again floating in Cottonwood. Juveniles could be regularly found for one to a few days after metamorphosis, in damp places under rocks or boards within a few meters of the water from which they emerged.

V. Tadpoles as Predators and Prey

Spadefoot Tadpoles as Predators

S. intermontanus tadpoles are facultative carnivores. In the field, tadpoles 2.9 cm long and longer were observed to prey upon larval Bufo

punctatus (1.2-2.8 cm) as well as conspecifics (1.5-4.1 cm); the latter activity should tend to select for early, synchronous reproduction. Hungry captive tadpoles (3.3-3.9 cm) consumed live conspecific hatchlings (0.8 cm) and, less readily, conspecific eggs, nearly hatched B. punctatus embryos (0.35 cm) and both freshly hatched and slightly older B. m. microscaphus larvae. B. punctatus eggs were invariably rejected as food items, although silt adhering to egg envelopes was sometimes nibbled away.

Scaphiopus tadpoles (species hammondi) are known to be very effective predators on mosquito larvae (Wright & Wright, 1949).

Spadefoot Tadpoles as Prey

Great Basin spadefoot larvae are relatively large (mature body length = 2.1-3.8 cm, total length = 5.0-9.0 cm), active, and fast growing tadpoles. As such, they are predicted to be relatively immune to predation by aquatic invertebrates. However, hydrophilid beetle larvae were observed carrying freshly dead spadefoot tadpoles (0.8 and 1.3 cm long) in their formidable jaws on two occasions. Dead and still struggling spadefoot larvae (to 5.7 cm in length) were also observed to have been captured by the large aquatic larvae of a fly, Tabanus punctifer. This species has been observed to prey upon newly metamorphosed Scaphiopus multiplicatus (1.5-2.0 cm long) near Portal, Arizona (Jackman et al., 1983).

The remains of adult S. intermontanus have been recorded in coyote scats collected at Jacob's Lake, Arizona (Wright & Wright, 1949). The stomachs of two coyotes trapped near a reservoir in the lower Hurricane Valley (northwestern Arizona) were found to be full of large tadpoles, undoubtedly those of S. intermontanus (Neal Middlebrook, BLM Arizona Strip District Biologist, pers. comm.). Based on circumstantial evidence, a dense concentration of 5.0-5.5 cm long S. intermontanus tadpoles occupying the shallow remains of a cattle tank (to 10 cm deep) was preyed upon by ravens

(footprints encircling the pool) and a golden eagle (flew up from the pool, crop distended) (Todd Soderquist, Arizona Game and Fish Dept., pers. comm.). Ravens (one or more) were also implicated in the disappearance of several dozen S. intermontanus tadpoles from Coyote Spring. The tadpoles occupied silty, shallow (2-4 cm deep) depressions dependably filled by overflow from a trough; after their disappearance, raven tracks were concentrated around the area previously occupied by tadpoles. Wood (1935) reports finding S. intermontanus tadpoles in the stomachs of garter snakes (Thamnophis sp.) near Vernal, Utah. The garter snakes were captured near the remains of a small roadside pool, holding a "solid mass of stranded, writhing spadefoot larvae."

Tiger salamander (Ambystoma tigrinum) larvae may also be important predators on spadefoot tadpoles over much of the study area, based on the following pieces of information:

- 1) Field studies indicate that Ambystoma larvae can significantly reduce and even eliminate entire tadpole cohorts (Calef, 1973; Seale, 1980).
- 2) Habitat overlap between A. tigrinum larvae and S. intermontanus tadpoles is predicted to be high. Like Scaphiopus, Ambystoma salamanders were found to breed in a variety of permanent and ephemeral tanks and pools from 1300 meters to at least 1800 meters in elevation. In the Rocky Mts., A. tigrinum occur to above 11,000 feet (3350 m) (Stebbins, 1966). Tiger salamander larvae are commonly planted in permanent and ephemeral cattle tanks in the study area by local residents, who harvest them at a later date for use or sale as fish bait.
- 3) Seasonal overlap between A. tigrinum larvae and spadefoot tadpoles is also predicted to be high. These salamanders typically breed somewhat earlier than spadefoots, giving their larvae time to grow before spadefoot hatchlings appear. On the study area at Pipeline Pond (1700 m), Ambystoma bred on or before the evening of 12 April in 1983 (water temperature at 1330 hours on 13 April = 12⁰ C.); nearly all eggs had hatched by 27 April (water temperature

at 1300 hours = 13⁰ C.). At Ivanpatch Tank (1650 m), Ambystoma larvae had grown to 6-10 cm in length by 17 May (water temperature at 1100 hours = 22.5⁰ C.); a few Scaphiopus tadpoles present on this date were 1.25 cm long. Especially in reliable waters, neotenic Ambystoma (large, predaceous, sexually-mature larval morphs) may be present throughout the year.

4) Late May surveys of stock tanks deemed suitable for breeding by spadefoot toads (Parashaunt and Mainstreet Valley areas, Arizona) showed low co-occurrence of spadefoot tadpoles and salamander larvae. Of fourteen tanks, one held both species (Ivanpatch Tank, above), nine held only Ambystoma, and four held only Scaphiopus.

BUFO PUNCTATUS

I. Distribution

Bufo punctatus is quintessentially a toad of the arid southwest, occurring east to central Texas, north to central Utah, and west through the deserts of southeastern California. In Mexico it extends south to Hidalgo and the tip of Baja California (Stebbins, 1966).

II. Breeding Habitats

Red-spotted toads bred successfully at all study sites below 1700 m in elevation (Table 2). Blair (1955) described Bufo punctatus as widely distributed in this same general area (environs of the Virgin River and its tributaries) below approximately 4400 feet (1350 m). Tadpoles were found along silty, gravelly and rocky sections of streambeds, and in reliable and intermittently-filled cattle tanks, ditches, potholes and elevated metal

cattle troughs. Only troughs which had rough cedar posts pounded into the ground at their perimeters (for stability) were used for breeding, presumably because they provided the traction needed for toads to climb up into the tanks. This species occurs below sea level in Death Valley (Turner, 1959), and up to 6500 feet (2000 m) over the entirety of its range (Stebbins, 1966).

Reflecting their widespread occurrence, B. punctatus tadpoles developed successfully over the full range of orthophosphate and nitrate/nitrite concentrations recorded in this study, and all but the lowest values of total dissolved solids and alkalinity (Figs. 2,3).

III. Egg and Larval Microhabitats

Red-spotted toad eggs are deposited in loose, flat masses (20-several hundred eggs/mass) on bottom materials: silt, litter, sand, gravel or matted vegetation (Table 6). Eggs typically were found in 2-4 cm of water (range = 0.5-8.5 cm), within 30 cm of land (range = 0-150 cm). Along streams, ovipositing toads strongly favored areas of still or slowly moving water: pools at the channel edge, semi-isolated backwaters, and shallow depressions on emergent gravel bars.

Several different factors may maintain this preference for shallow, protected, slow-moving water. First, eggs placed in such sites are less likely to be carried away by the current or damaged by materials floating downstream. Second, larvae hatching from eggs placed in relatively sequestered locations may enjoy a measure of protection from predators (see Section V). Finally, such placement may frequently speed development of both eggs and newly hatched larvae by exposing them to higher temperatures than occur in deeper/faster water: B. punctatus eggs have been shown to develop 7-8 times faster to Gosner stage 20 at 32.2° C. than at 17.1° C. (Zweifel, 1968). Tevis (1966) states that water temperatures at B. punctatus eggs laid

along a rocky stretch of stream near Palm Desert, California often exceeded that of the main current by 2° C. Egg microsite temperatures exceeded control temperatures in 20 of 32 such comparisons made at streams and tanks in the present study (Table 7). The greatest temperature difference observed was 10.5° C., at Middle Spring; the mean difference, based on all comparisons, was 1.7° C. A high proportion of Red-spotted toad eggs develop normally at temperatures up to 32° - 33° C. (Portal and Mesa, Arizona eggs); older embryonic stages (Portal, Arizona) may survive temperatures up to at least 36.4° C. (Ballinger & McKinney, 1966; Zweifel, 1968). Temperatures exceeding 33° C. were rarely recorded at any site in the course of this study, even in very small, sunny, isolated pools (e.g. cow hoofprints), and there was no evidence that eggs failed to develop at any site because of overheating. Shallow, peripheral egg placement is, however, predicted to increase the likelihood that eggs are lost to dessication or trampling by livestock. The former was documented to occur only three times over the course of this study (which emphasized reliable waters): twice in late July/early August along a very shallow stretch of water at Grapevine which had been commonly utilized for breeding all season, and once in August at the edge of the ephemeral tank at Coyote. Trampling of eggs by cattle was observed at Ft. Pierce, Middle, White Saddle and Grapevine, but entailed few eggs at any site.

B. punctatus typically remain aggregated at the site of egg placement until they have reached 8 to 10 mm in total length (3.4-4.0 mm in body length). Older tadpoles occur at all available depths, but are most commonly found from 1-6 cm, in relatively quiet water. Shallow water may be selected by Red-spotted toad tadpoles both for its warmth and (especially in very warm, still or polluted waters) relatively high oxygen tensions: toad tadpoles (Bufo terrestris) have been shown to have high metabolic and oxygen consumption

rates, while lacking (as a group) functional lungs until metamorphosis (Noland & Ultsch, 1981). Tevis (1966) reports that once limb buds appeared, B. punctatus tadpoles aggregated in dense masses at the shoreline during the heat of the day: "Often they pack themselves so tightly that they are aligned in ranks facing the margin; and even when at the very edge they keep struggling forward to push their backs out of the water." The tadpoles occupied a progressively drying but still actively flowing stream. No comparable behavior was observed in the present study, perhaps because thermal gradients were less steep at study site locations. Beiswenger (1978) reports that bufonid tadpoles aggregate at a preferred subset of temperatures along a laboratory temperature gradient, e.g. 28⁰-34⁰ C. along a gradient of 22⁰-40⁰ C. (B. boreas, B. hemiophrys), and 27.5⁰-37⁰ C. along a gradient of 11⁰-42⁰ C. (B. americanus). The upper preferred limits for B. boreas and B. americanus are within 3⁰ C. of the lethal temperature ranges for these species .

IV. Temporal Patterns

Breeding Patterns

Table 8 lists the extreme dates on which clutches were laid at study sites. As with S. intermontanus, earliest oviposition dates occur later at higher elevations, suggesting that reproduction is initially limited by temperature. Tevis (1966) reports that evening air temperatures of 18⁰ C. or greater were required for surface activity in his Deep Canyon, California population of Red-spotted toads, and that breeding commenced when temperatures reached or exceeded 24⁰ C. Death Valley, California B. punctatus have been observed to delay breeding until mean daily temperatures reach approximately 21⁰ C. (Turner, 1959). While egg laying in this species may be directly controlled by air temperature, water rather than air temperatures are expected

to control the success of egg development. The lower limit for viable development of Red-spotted toad eggs has been variously established as approximately 21⁰ C. (Hays County, Texas eggs), less than 18⁰ C. (Mesa, Arizona eggs), and lying between 13.6 and 17.1⁰ C. (Portal, Arizona eggs) (Ballinger & McKinney, 1966; Zweifel, 1968). Only one instance of selection apparently operating against premature reproduction at unsuitably low temperatures was observed in this study, along the spring-fed stream running down upper Frehner Canyon (north side, Virgin Mts.) on 15 May. About a third of a clutch of B. punctatus eggs distributed across a shallow pool was moldy, with the rest unhatched. The water temperature in full sun at the eggs was 15.5⁰ C. at 1400 hours.

Table 9 summarizes the temporal distribution of clutches at study sites. Reproduction peaked in late April-early May at the lowest and late May-early June at the highest elevations, and then gradually declined through August (July at the highest elevations). While rainfall often stimulates breeding, it is not required as a proximate cue for reproduction when water is otherwise available. In this study, many clutches occurred in June, by far the driest month, and dozens of amplexic pairs were found over the entire course of the summer when no rain had fallen for at least the previous week. Both Tevis (1966) and Turner (1959) report that this species breeds independently of the stimulus of falling rain.

Adult and Juvenile Diurnal Occurrence

Mating pairs are commonly observed during the day at the height of the breeding season. Males also sometimes call diurnally at this time. Otherwise, adults generally remain inactive during the day, seeking shelter in rock crevices (Stebbins, 1951), under boards or in "covered subterranean recesses" (Turner, 1959), or beneath thick piles of brush. When surface water is unavailable, these toads may remain in underground burrows for long periods

of time (Stebbins, 1951; Tevis, 1966). Juveniles were encountered sporadically at all reliable waters, primarily from June through August. Hundreds of juveniles were occasionally found at the edge of temporary, rain-filled cattle tanks (under rocks, in the open, and in mud cracks) soon after having transformed. This apparently reflected both highly synchronized egg laying and low predator densities in these previously dry tanks.

V. Eggs and Tadpoles as Prey

Bufonid eggs have been shown to be unpalatable or toxic to a variety of potential natural predators: salamanders (Ambystoma gracile), several species of fish (Gasterosteus aculeatus, Salmo clarkii, Lepomis sp., Ictalurus melas), two species of snake (Salvadora lineata, Opheodrys aestivus), leeches (Haemopsis sp.) and S. intermontanus tadpoles (Licht, 1968, 1969; this study). Garter snakes (Thamnophis sirtalis), which are known to successfully prey on adult toads, suffered no ill effects after ingesting B. valliceps eggs; it is not known if these snakes eat toad eggs under natural conditions (Licht, 1968).

B. punctatus tadpoles, particularly early larval stages, appear to be highly liable to predation based on the following pieces of information:

1) Freshly killed, or in some cases still living Red-spotted toad tadpoles were found at various times in the jaws of each of the three most abundant classes of potential predators occurring at various study sites: notonectids, odonate naiads (both dragonflies and damselflies), and spadefoot tadpoles. All of these groups showed complete temporal overlap with B. punctatus tadpoles in permanent waters. Invertebrate predators may successfully capture toad tadpoles longer than themselves, e.g. a still living 1.7 cm tadpole in the jaws of a 1.2 cm damselfly larva, and a freshly dead 1.4 cm tadpole in the jaws of a 1.0 cm notonectid.

2) At two sites, young toad larvae disappeared from areas in which predators were observed (sections of the main channel at Ft. Pierce, crowded with 1-3 cm long Scaphiopus tadpoles; a deep pool at Maple, holding at least one large (4-5 cm) dragonfly naiad) while remaining abundant in adjacent areas free from predators (segregated side pools at Ft. Pierce; a small, gravelly depression just downstream from the pool originally holding most of the eggs, at Maple). Seale (1980) ascribes the complete disappearance of an estimated 200,000 B. americanus hatchlings for two consecutive years at a Missouri pond to predation by salamander (Ambystoma tigrinum) larvae, which grew to a maximum of nearly 9 from a maximum of 2.5 cm over the course of the disappearance.

3) The reproductive success of B. punctatus at permanent waters, with large predator populations, was always very low. Less than 0.2 percent of hatchlings were found to survive on the average to metamorphosis; many clutches were entirely unsuccessful. In contrast, the reproductive success of toads at temporary waters, with low predator densities, was at least sometimes very high (see previous section).

B. punctatus tadpoles are probably too small (mature body length = 1.2-1.6 cm; total mature length = 3.4-4.0 cm) to be highly sought as food by predatory birds and mammals. The predatory impact of snakes, and in appropriate areas turtles and bullfrogs (Rana catesbeiana) remains unknown.

BUFO W. WOODHOUSEI/BUFO M. MICROSCAPHUS

I. Distribution

Bufo w. woodhousei is widely distributed, ranging from within a few hundred miles of the Canadian border to southern Texas, as far east as central Missouri, and as far west as the Columbia River in south central Washington. By comparison, Bufo m. microscaphus is known from only a few areas of the

United States and Mexico, primarily in the upper Colorado and Gila River drainages (Stebbins, 1966). The two species co-occur and hybridize at a number of locations in Arizona and Utah including, in the vicinity of the study area, sites along the Virgin River from Harrisburg Junction, Utah, to approximately Littlefield, Arizona (Stebbins, 1951; Blair, 1955). In areas of sympatry, the two species are best distinguished by the ratio of parotoid gland length:width and the relative development of cranial crests (Blair, 1955).

II. Breeding Habitats

Toads belonging to this species complex were found at three study sites: Grapevine, Ft. Pierce, and Middle. Of these only the Grapevine population can be unequivocally classified as B. w. woodhousei (N = 11 adults). The Middle Spring population is typically B. w. woodhousei except for the occurrence of short, microscaphus-type parotoids (3 of 7 adults). The Ft. Pierce population predominantly resembles B. m. microscaphus, but does feature such woodhousei-type characters as relatively elongated parotoids (2 of 5 adults) and moderately developed cranial crests (1 of 5 adults).

All three sites are highly reliable, shallow, clear-flowing streams, with substantial cover provided by riparian shrubs and/or trees. Elevations vary from 520 to 1295 m (Table 2).

In Oklahoma, at the eastern edge of its range, B. w. woodhousei has been reported to commonly breed in a variety of shallow (usually 25 cm or less) aquatic habitats: the muddy backwashes of rivers and creeks, floodplain sloughs, and the shallower portions of ditches, flooded fields and cattle tanks (Bragg & Smith, 1942). In contrast, New Mexican B. w. woodhousei were found to utilize only shallow, slow-flowing sections of streams, and on one occasion, clear, grassy "quarry-pools"; cattle tanks, roadside ditches, and

even spring-fed pools near the stream sites were never used (Bragg, 1941). Along the Virgin River, Blair (1955) concluded that B. w. woodhousei prefers still or relatively slow-moving waters (ponds, flood plain marshes and sloughs), while B. m. microscaphus prefers the relatively rapid flow of streams. He recognized that competition may be reinforcing these differences, however: populations of B. m. microscaphus were found at a number of reservoirs, for example, in the absence of B. w. woodhousei. In southwestern Utah, B. w. woodhousei occurs up to at least 5200 feet (1585 m), while B. m. microscaphus occurs up to at least 5800 feet (1770 m) (Blair, 1955). Over the entirety of its range, B. w. woodhousei has been found up to 8500 feet (2600 m) (Stebbins, 1966).

Toads of this group were found breeding over a wide range of total dissolved solids, alkalinities, and orthophosphate concentrations, and the entire observed range of nitrate and nitrite concentrations (Figs. 2,3). There is no reason to expect that breeding was limited by unsuitable water chemistry at any study site.

III. Egg and Larval Microhabitats

Eggs of both species are laid in long strings (to 4 or more m) contained within a gelatinous envelope. Strings are unanchored, except incidentally when caught around rocks or vegetation, and commonly are displaced and fragment into shorter segments in fast or moderately flowing water. Eggs were found in shallow water near the edge of the main channel of small streams (Grapevine, Ft. Pierce), and in a similar situation along the side channel of a larger stream (Beaver Dam Wash) (Table 10). The minimum and maximum temperature tolerances of B. w. woodhousei eggs collected in Texas, Oklahoma and Kansas have been respectively estimated to be 15.3⁰ C., and

35° C. (Volpe, 1953). In this study, water temperatures at eggs paralleled those of the main current, ranging from 20° to 24° C. (Table 11).

Newly hatched tadpoles (Gosner stage 17) can maintain a stable position in even relatively fast currents (e.g. 25 cm/sec at Ft. Pierce) by means of a ventral adhesion organ. This "oral sucker" develops in most if not all species of North American tadpoles, but is lost at approximately the time that most hatch (Gosner, 1960). Older woodhousei/microscaphus tadpoles (past Gosner stage 18) were not observed at any study site. This may reflect the confounding presence of large numbers of B. punctatus tadpoles at all three sites, as well as losses to predators (see section V). Trampling of young tadpoles by cattle accounted for very minor losses at Ft. Pierce.

IV. Temporal Patterns

Breeding Patterns

April and May were the peak months for breeding at all three study sites. Eggs or mated pairs were observed from 24 April to 19 May at Grapevine, from 23 April to 4 May at Ft. Pierce Wash, and on 25 May at Middle Spring. Eggs were also found on 16 April at lower Beaver Dam Wash (elevation 570 m). Many recently transformed juveniles and rapidly maturing tadpoles (most closely resembling B. m. microscaphus) were found along approximately 1.5 km of the upper Beaver Dam Wash on 17 June, suggesting that eggs had been laid on this site no later than May. No eggs or young tadpoles were found on this date.

Wright & Wright (1949), who do not distinguish between B. m. microscaphus and B. w. woodhousei, state that the latter breeds from March to July, with tadpoles transforming from late March to September. In Oklahoma, B. w. woodhousei has been characterized as "breeding early in the springtime regardless of rain but also breeding at any time to early fall with any

considerable rains which fall" (Bragg, 1945). In New Mexico, B. w. woodhousei was also found to breed independently of rainfall, with tadpoles observed abundantly in June and again (at one site) in late August (Bragg, 1941). The earliest possible date of spring breeding is presumably determined by temperature: in Oklahoma, Bragg & Smith (1942) report that B. w. woodhousei rarely initiates breeding below 13⁰ C. Furthermore, if temperatures drop once pairs have formed, females delay ovipositing until conditions become warmer.

Adult and Juvenile Diurnal Occurrence

Adult B. w. woodhousei at Grapevine and Middle Springs could be dependably found during the day from April through at least August, resting quietly near or under cover (boards, dense stands of Typha or Baccharis) in or by shallow water. At Ft. Pierce, adult B. m. microscaphus were observed diurnally only at the height of breeding, in late April and early May. This difference may reflect variation among habitats rather than species, however: the best cover at Ft. Pierce occurs somewhat away from the stream (where field work was concentrated) among dense, shrubby Baccharis and Tamarix.

V. Tadpoles as Prey

At Ft. Pierce, S. intermontanus tadpoles (1.2-4.0 cm) fed avidly on the silty, gelatinous surface of the tubes containing B. m. microscaphus eggs. When holes appeared, the spadefoots took freshly hatched toad tadpoles (2.5 mm) into their mouths and even carried them off for short distances, but then spit them out or dropped them. Hungry captive spadefoot tadpoles (3.3-3.9 cm) were found to be less fussy, consuming both 2.6 mm (Gosner stage 17) and 7.0 mm (Gosner stage 20) microscaphus tadpoles with no apparent ill effects.

Both B. w. woodhousei and B. m. microscaphus tadpoles are probably highly susceptible to predation. Like B. punctatus, they are usually hatched by Gosner stage 16 or 17, well before they are capable of swimming away from potential threats. In addition, both mature at a relatively small size (Beaver Dam Wash B. m. microscaphus, the largest of the three species, mature at a body length of 1.6-1.8 cm), and, to probably a more universal degree than B. punctatus, breed at permanent waters hosting large invertebrate populations, salamander larvae, crayfish, and even fish (e.g. along Beaver Dam Wash). To offset these impediments to larval survival, B. w. woodhousei in particular is remarkably fecund. While a female B. punctatus may produce 1,000-3,000 eggs (Wright & Wright, 1949), B. w. woodhousei females may produce well in excess of 25,000 eggs (Smith, 1947). When coupled with fairly synchronous reproduction, such enormous fecundity may function as a predator satiation mechanism. At the least, it suggests that the major selective factor shaping reproduction in this species has not been tadpole competition.

HYLA REGILLA

I. Distribution

Pacific treefrogs occupy moist habitats in far western North America from southern British Columbia to the tip of Baja California. They occur eastward to western Montana, central Idaho, eastern Nevada, and northwestern Arizona (Stebbins, 1966). Their abundant presence at Middle Spring, documented in the course of this study, extends the range of this species 28 or more km southeast of the populations "found calling in choruses with B. woodhousei in the lower Virgin drainage" by Blair (1955).

II. Breeding Habitats

Middle Spring was the only study site to support a breeding population of Pacific treefrogs. A single male H. regilla was heard repeatedly at White Saddle Spring late in the afternoon of 14 May, but treefrog eggs or tadpoles were never observed there.

Pacific treefrogs have been found to one-half mile (one km) from water, and may seek cover in a variety of fissures, culverts and crannies away from its immediate environs (Stebbins, 1951). This species is, nevertheless, essentially mesically adapted. Pacific treefrogs have the smooth skin associated with primarily aquatic amphibians. They lack the specialized morphological, physiological and behavioral traits which allow Scaphiopus and Bufo species to survive the disappearance of surface water by burrowing. Their characteristic habitat is described as "the ground, especially about streams, springs, ponds, swamps, and other moist places" (Wright & Wright, 1949), or "low plant growth near water" (Stebbins, 1966), or "damp recesses among rocks and logs; the ground in the vicinity of springs, streams and lakes; rank growth of vegetation, especially in marshy places" (Grinnell and Camp, 1917, quoted in Wright & Wright, 1949). Cunningham & Mullally (1956) report that few newly metamorphosed H. regilla are found "where the vegetation is sparse or the soil is not damp."

The spring habitat at Middle Spring offers both dependable surface moisture and abundant low vegetative cover. Its waters proportionally varied the least of any site in terms of alkalinity and total dissolved solids, implying that it enjoys the most constant summer discharge rate (Appendices 1,4). Cover is provided in the wettest areas by dense rushes (Juncus sp.) and water cress (Rorippa nasturtium-aquaticum), and in drier areas by a low-growing perennial herb, Anemopsis californica, and thickets of seep-willow, Baccharis glutinosa. Both the rushes and cress were sometimes

grazed severely by cattle over the course of the summer, but recovered rapidly when grazing pressure was alleviated. A. californica, a very strong-smelling plant, was not significantly consumed by cattle, while seep-willow thickets were only peripherally browsed.

H. regilla occurs from sea level (Stebbins, 1951) to at least 11,600 feet (3535 m)(Schechtman & Olson, 1941). This remarkable altitudinal range is paralleled by the adaptability shown by tadpoles in surviving a wide range of environmental temperatures. Early larval stages (gastrulae and neurulae) obtained from a Los Angeles stream developed normally after being frozen within a block of ice overnight (Schechtman & Olson, 1941). In nature, tadpoles have been found in water as warm as 34.0°C ., in ponds and marshy areas at Tioga Pass in Yosemite National Park, where tadpoles were concentrated in the warmest, shallowest available areas (Cunningham & Mullally, 1956). In the laboratory, the incipient lethal temperature for tadpoles acclimated to 27.5°C . was found to lie between 36° and 37°C . (Brown, 1969).

Like their larvae, adult Pacific treefrogs may survive both being frozen and being heated to 37°C . for short periods of time. In distinct contrast, however, their preferred body temperature is less than 24°C . (Cunningham & Mullally, 1956). It follows that Pacific treefrog habitat should ideally provide water that is relatively warm for optimal larval development (from late February-September in this study) and relatively cool for adult thermoregulation, particularly in mid-summer. At Middle Spring, midday water temperatures varied less than at any other site in this study: higher (at 19.0°C .) than all but the two lowest elevation sites in late April, and probably quite near to the preferred adult temperature (at 19.0 - 20.5°C .) throughout the summer (Appendix 5). Comparable temperature

ranges were also recorded at sites at which Pacific treefrogs did not occur, however, notably Grapevine (20-25⁰ C.) and Black Rock (15-24⁰ C.) (Appendix 5).

Middle Spring water was found to be unusually low in total dissolved solids, high in alkalinity (i.e. bicarbonate), and high in nitrate and nitrite relative to other waters in this study (Figs. 2,3; Appendices 1,2,4). Any of these factors may but probably do not bear critically on the unique occurrence of Pacific treefrogs at this study site. Based on observations at hot springs, Brues (1932) concluded that H. regilla breeds at waters of cool-moderate temperature (up to 33.4⁰ C.), low-moderate alkalinity, and low-moderate salinity.

III. Egg and Larval Microhabitats

Pacific treefrog eggs occur in small clusters (2-12 eggs/cluster in this study), encased within a common envelope which is usually loosely attached to vertical plant stems or floating algae. Eggs were found from just below the water surface to 7 cm depth, usually within 15 cm of the shore in shallow (less than 10 cm deep), slow-moving water (Table 10). The envelope and its contents commonly float if detached from anchoring vegetation, at least in the early stages of development. In lieu of aquatic vegetation, eggs were also found attached to silt or sand grains at the bottom of a pool.

The shallow depths at which eggs are anchored, and their placement in shallow, slow-moving water commonly results in the eggs experiencing warmer temperatures than if placed randomly (Table 11). The mean temperature difference between egg sites and the main current is 1.5⁰ C. (N = 4). The occurrence of eggs in quiet water may also reflect selection against laying eggs where they are likely to be displaced by the force of a current and float downstream.

Tadpoles of all ages were typically found resting on the bottom or swimming slowly in shallow (1-4 cm), quiet water. At various times they were observed on sunny, bare patches of sand or silt; directly at the water's edge under overhanging grass; under matted algae, in moderately fast-flowing water; and feeding at the surface of aquatic plants in the depressions created by cattle hooves. Tadpoles occurred alone and in loose aggregations. The latter presumably develop in response to thermal gradients or favorable feeding opportunities.

IV. Temporal Patterns

Breeding Patterns

Over the entirety of their range, Pacific treefrogs may breed as early as January (Wright & Wright, 1949; Stebbins, 1951, 1966). At Middle Spring, breeding probably commenced in late February in 1983 (eggs developed to Gosner stage 17 were present by 4 March, 1984). On 7 April, 1983, when the site was first sampled, tadpoles to 2.1 cm total length were present. Eggs were abundant through mid-May, with steadily diminishing numbers observed through 3 July. Transforming tadpoles occurred from late May through the third week of September. The maximum interval from hatching to transformation in mid-late summer was approximately 78 days. Larval development may be completed in as few as 50 days (Wright & Wright, 1949).

Adult and Juvenile Diurnal Occurrence

Stebbins (1951) reports that this species is active year round, at least at lower elevations. At Middle Spring, adults and second season juveniles were observed diurnally, usually in great numbers, over the entire course of this study (early April to early October). Males were heard sporadically during daylight hours in the spring (April-early May) and again in the fall (late September-October). Cunningham & Mullally (1956) report

that males commonly call during the day at the height of the breeding season. On 13 January, 1984, a few males were in chorus at Middle Spring at 1130 hours under an overcast sky, at an air temperature of 5° C. and a water temperature of 16° C.

V. Eggs and Tadpoles as Prey

It is estimated that fewer than 4 percent of the Pacific treefrog eggs laid over the course of this study developed to metamorphosis. The numerical contribution of predation to egg and larval mortality is, however, unknown. The palatability of H. regilla tadpoles to potential predators has not been established, although eggs and adults have been shown to be palatable to cutthroat trout (Salmo clarkii) (Licht, 1969). Within this same genus, H. crucifer tadpoles have been shown to be palatable to dytiscid beetle larvae, giant water bug nymphs and adults, larval Ambystoma salamanders and adult Notophthalmus salamanders (Brodie & Formanowicz, 1983), and H. gratiosa tadpoles to Ambystoma larvae and dragonfly naiads (Caldwell et al., 1980). Three potential predators are common at Middle Spring: dragonfly naiads, damselfly naiads and hydrophilid beetle larvae.

The following aspects of Pacific treefrog biology may all act to reduce predation: 1) Embryos typically hatch late in Gosner stage 20, at which time they are capable of rapid, well-coordinated swimming. 2) Tadpoles conceal themselves at sundown under bottom sediments and litter (Cunningham & Mullally, 1956). 3) Tadpoles hatching early in the season may develop to a relatively large size before many insect predators appear. For example, ovipositing damselflies were first observed at Middle Spring on 14 May. By 25 May, damselfly naiads to 10 mm in length were plentiful, the commonest predaceous insect at the site. On this same date, however, some treefrog tadpoles were beginning to metamorphose and many others exceeded 30 mm in

total length. At least under experimental conditions, small, recently hatched hylid and ranid tadpoles have been found to be most liable to predation by small salamanders and most invertebrates (Caldwell et al., 1980; Brodie & Formanowicz, 1983).

HYLA ARENICOLOR

I. Distribution

Canyon treefrogs range from southern Utah to northern Oaxaca, Mexico, east to central New Mexico, and west to the Arizona-Nevada border. Isolated populations occur in the Davis and Chisos Mountains of west Texas. This species has been found up to approximately 9000 feet (2750 m) (Stebbins, 1966).

II. Breeding Habitats

A breeding populations of Canyon treefrogs was found at only one study site: the upper, mostly perennial segment of stream fed by Maple Spring. The stream consists of a series of roughly bathtub-sized pools (20-55 cm deep in May), sometimes alternating with short sections of narrower channel. Much of the stream is partly or entirely shaded by shrubs and trees and a steeply ascending south bank. Both banks are thickly studded with large rocks and boulders.

Adults and juveniles were invariably found perched quietly on streamside rocks (or, very rarely, logs), with their legs drawn up close to their bodies. In this catlike posture they are extremely cryptic, resembling the rocks on which they sit. Both sunny and shaded sites are utilized, with the former strongly favored on all but the hottest afternoons in June and July. Wylie (1981), working with a Graham County, Arizona populations of H.

arenicolor, found that basking treefrogs could and did achieve body temperatures higher than the ambient air temperature, up to at least 35.8°

C. He suggests that basking may be multiply advantageous to this species, in contributing to an exceptionally rapid postmetamorphic growth rate, maximizing the efficiency of adult and juvenile digestion, and discouraging predation by less heat-tolerant species, notably snakes. When disturbed, Canyon treefrogs typically leap from their resting places to the nearest deep water, where they may remain submerged on the bottom, retire beneath an overhanging boulder, or simply swim to the edge, including the one nearest to the disturbance (and their previously chosen basking site).

Across their range, Canyon treefrogs typically occur in the immediate vicinity of water along perennial or intermittent, rocky streams (Wright & Wright, 1949; Stebbins, 1951, 1966). They may also be found along "irrigation ditches" (Wright & Wright, 1949), and have been documented to breed successfully in rain-filled potholes (Zweifel, 1961). On rainy or overcast days they may be found hopping about actively several hundred meters from their home stream (Wylie, 1981).

As compared with other sites in this study, Maple Spring water was quite saline, highly alkaline, and low in nitrate, nitrite, and orthophosphate (Figs. 2,3; Appendices 1-4).

III. Egg and Larval Microhabitats

Canyon treefrog eggs were found attached singly and in small flat clusters to bottom materials in shallow (most typically 2-4 cm), unshaded, slow-flowing water (Table 10). Water temperatures at eggs were consistently higher than those of the main current or adjacent, deeper water, with a mean recorded difference of 2.6° C. (N = 5) (Table 11). This difference may have critically facilitated egg development, in that control stream temperatures

were consistently lower, at 12° - 12.5° C., than the minimum viable limit of 13° C. tentatively established by Zweifel (1968). Even so, from 10 to 88 percent of the eggs laid in May clutches at Maple Spring failed to hatch (N = 4 clutches). In Wylie's (1981) study, Canyon treefrogs oviposited in shallow portions of a stream, semi-isolated side pools, and wholly isolated nearby pools. Egg deposition sites were on the average 0.6° C. (shallow stream), 6.7° C. (semi-isolated pool) and 8.8° C. (isolated pool) warmer than the main stream flow. Egg viability increased with increasing temperature: on the average, 91.2 percent of eggs in stream clutches developed (at a mean recorded temperature of 19° C.) versus 96.9 percent of semi-isolated pool clutches (at a mean recorded temperature of 23.5° C.) and 100 percent of wholly isolated pool clutches (at a mean recorded temperature of 25.9° C.). Conversely, the frequency with which some or all of the resulting tadpoles were killed by dessication was least in the stream (0 of 18 clutches), intermediate in semi-isolated pools (6 of 9 clutches) and highest in isolated pools (7 of 8 clutches). Canyon treefrog eggs have been shown to develop 5.6 times faster to Gosner stage 20 at 29.1° C. than at 15.5° C., with the upper limiting temperature for successful egg development estimated to be 31° C. (Zweifel, 1968).

Tadpoles most frequently occurred at depths of less than 10 cm, but were observed at times to at least 30 cm, resting quietly on the bottom or feeding at the surface of rocks, on bottom materials, or on floating, filamentous algae. Individuals occurred singly and in loose aggregations.

IV. Temporal Patterns

Breeding Patterns

Eggs were deposited at Maple Spring from approximately 29 April to 14 June. In southeastern Arizona at 1320 meters, earliest oviposition dates over

a three year period ranged from 7 to 23 May, with breeding peaking in May and June, and clutches appearing as late as 1 August (Wylie, 1981). In the Chiricahua Mountains of extreme southeastern Arizona (South Fork, Cave Creek), Canyon treefrogs were found to breed in May, when stream flow is high from melting snow, and/or late June and early July, when stream flows are replenished by thunderstorms (Zweifel, 1961). Both Wright & Wright (1949) and Stebbins (1951) state that the breeding season of this species extends from early March to July.

Where surface water is available in the spring, the onset of reproduction is probably determined by temperature. Wylie (1981) found that in his southeastern Arizona population, males began to call when evening water temperatures exceeded 13⁰ C. It may be recalled that this temperature constitutes the lower limit for successful egg development, according to Zweifel (1968). Both chorusing by males and oviposition by females commonly occurs independently of precipitation per se. Even at previously dry sites, female H. arenicolor may not lay eggs until several days after pools have been filled by rainfall (Zweifel, 1961).

Newly transformed treefrogs appeared at Maple Spring by the end of the first week in July, suggesting that a minimum of 70 days was required from egg deposition to metamorphosis. This agrees closely with the 70-74 day minimum development periods reported by Wylie (1981). In the Chiricahuas in late summer, at presumably higher temperatures than in the previous two cases, H. arenicolor tadpoles minimally required 50-60 days for full maturation from the time of oviposition (Zweifel, 1961). Stebbins (1951) states that the larval period extends for 40-75 days in this species.

Adult and Juvenile Diurnal Occurrence

Adult Canyon treefrogs were regularly observed during the day at Maple Spring from early May to late September. No individuals occurred at

midmorning on 9 April (water temperature = 6° C.) despite bright sunshine suitable for basking. This species has been reported to be active as early as February near St. George, Utah, at an elevation of approximately 900 m (Tanner, 1931, quoted in Wright & Wright, 1949). At 1320 m in southeastern Arizona, Canyon treefrogs were found to be active in all months except January or February, although not necessarily in all years. Peak adult abundance coincided with peak reproduction in May and June (Wylie, 1981).

V. Egg and Larval Mortality

Survivorship of three groups of eggs monitored at Maple Spring from before hatching to metamorphosis was approximately 1, 7, and 28 percent. Highest losses occurred in eggs (through failure to develop) and early larval stages (total length less than 2.0 cm). Estimated survivorship of tadpoles 2.0 cm long to metamorphosis ranged from 18 percent (2 of 11 tadpoles) to 77 percent (41 of 53 tadpoles). Fewer than 200 tadpoles were killed by pools drying along the course of the stream.

Egg and larval mortality in Wylie's (1981) study varied from 100 percent (in a drought year, when the entire study site dried before any tadpoles had metamorphosed) to 98 percent (in a more normal year). Following the drought year, the breeding population of treefrogs was reduced by approximately 50 percent as compared with the two previous breeding seasons. Besides dessication, the major apparent source of treefrog mortality at this site was predation by garter snakes (Thamnophis cyrtopsis). Of sixteen captured snakes having food in their stomachs, 62.5 percent had eaten H. arenicolor tadpoles, 19 percent had eaten transforming tadpoles, and 19 percent had eaten juvenile frogs.

Potential invertebrate predators on tadpoles at Maple Spring include dragonfly naiads (some of which were 4-5 cm long in early May, having

presumably overwintered in the stream), damselfly naiads, and hydrophilid beetle larvae. Irritating (to human mucous membranes) skin secretions probably help protect adult Canyon treefrogs from predation by mammalian and avian predators.

SOME MANAGEMENT CONSIDERATIONS

LARVAL ANURAN HABITAT REQUIREMENTS: A SUMMARY

Water Chemistry

Inappropriate water chemical parameters can limit the success of anuran reproduction. For example, immersion in both strongly acid and saline solutions interferes with water uptake into eggs, and results in hatchlings that are bent, runted, and characterized by abnormal locomotion and reduced activity rates (Gosner & Black, 1957). In this study, the repeated absence of tadpoles at Burro Spring (14.3 km SSW of Grapevine) may well reflect its high salinity. On 24 June, the specific conductance of Burro Spring water was 7000 micromhos, a value 75 percent greater than the next highest recorded in this study (at Coyote Tank). By comparison, Burro Spring water was found to be only modestly alkaline, at 120 ppm bicarbonate.

Water Temperature

Embryonic temperature tolerances may vary considerably within a given species as a function of geography and local rainfall patterns (Brown, 1966). Approximate viable ranges for some of the species considered in this report are as follows: 13-31⁰ C. (Portal, Arizona H. arenicolor); 16-33⁰ C. (Portal, Arizona B. punctatus); 15.3-35⁰ C. (Texas, Oklahoma and Kansas B. w. woodhousei) (Volpe, 1953; Zweifel, 1968). Such experimentally-determined

ranges, obtained by applying a 50 percent viability criterion to the development of eggs to Gosner stage 20 (gill circulation), are conservative in at least two respects. First, older embryonic stages are more thermally tolerant than younger stages (Schechtman & Olson, 1941; Brown, 1967; Zweifel, 1968). Second, survivorship may increase as the interval of exposure to extreme temperatures decreases (Schechtman & Olson, 1941; Brown, 1967).

Water temperatures near the upper thermal tolerances of eggs and larvae are predicted to be optimal, in promoting rapid development to metamorphosis. Reflecting this fact, frogs and toads typically place their eggs in sunny, shallow, slow-moving water; both bufonid and hylid tadpoles may also concentrate in such areas. These behaviors are also potentially disadvantageous, however, in that warm, shallow microsites are usually the first to completely dry when water levels decline.

Minimum Temporal Water Requirements for Tadpoles

In ephemeral aquatic habitats (e.g. potholes, many cattle tanks), desert anurans are expected to breed within a few days of the habitat filling with water, as long as temperatures are warm enough. The subsequent span of larval development is expected to vary at least with species, water temperature, and larval food quality. Minimum transformation times recorded in this study ranged from 18 days (S. intermontanus) to 70 days (H. arenicolor), with tadpoles from a single clutch typically metamorphosing over a period of two or more weeks.

The onset of breeding at permanent waters appears to be primarily controlled by species-specific adult and larval temperature tolerances. The subsequent temporal distribution of clutches will reflect such factors as the pattern of rainfall and its influence as a proximate breeding stimulus; the number of breeding females in a population; the interval to predictably cool

autumn temperatures; and any season-dependent agent of natural selection which mitigates against reproductive success. In this study, S. intermontanus eggs and larvae occurred at permanent sites from mid March-May to as late as mid July-October (Table 4); B. punctatus eggs and larvae occurred from mid April-May to as late as mid July-late September (Table 8); H. regilla eggs and larvae occurred from approximately late February-mid September; and H. arenicolor eggs and larvae occurred from late April-mid September. Assuming that B. w. woodhousei and B. m. microscaphus larvae require 40-60 days to mature, like those of B. w. fowleri (Wright & Wright, 1949), eggs and larvae of these species may have been anticipated to occur from mid April-May until at least the latter part of July.

Larval Food

As a group, tadpoles have fairly generalized feeding and food habits. They are equipped with rows of "labial teeth", which function as scrapers, and can remove particles from suspension by gill filters and a mucus-entrapment mechanism (Wassersug, 1972). Tadpoles will eat a wide range of blue-green and green algae (Dickman, 1968; Seale & Beckvar, 1980), bottom sediments (Nathan & James, 1972), and their own feces (Steinwascher, 1978). In captivity they thrive on pulverized rabbit chow (Seale & Beckvar, 1980), canned spinach and commercial fish food (Brown, 1969), and boiled lettuce supplemented with chopped worms, phyllopods, and uncooked beef, pork and lamb (Blair, 1955). While all species will probably scavenge dead animals, of North American forms only certain Scaphiopus species are known to be actively predaceous.

All tadpole diets are not equivalently nutritious. Seale (1980) found that natural populations of hylid and ranid tadpoles ingested suspended phytoplankton in preference to bottom sediments. Except at the lowest

densities of suspended particles, tadpoles could obtain more nutrients (organic nitrogen) from suspended than settled materials in a given period of time. Nathan & James (1972) found that bufonid tadpoles fed only pond mud suffered high mortality and retarded growth rates when compared to individuals fed pond mud and boiled lettuce. In laboratory experiments, a high protein:carbohydrate ratio was found to be the key element promoting growth of Hyla chrysoscelis tadpoles (Steinwascher & Travis, 1983). Captive Bufo americanus tadpoles grew faster on a diet of algae cultured on dead grass than on pond litter (Brockelman, 1969).

Natural populations of tadpoles may compete for food, if not limited by high predation rates. Data supporting this hypothesis have been presented by Seale (1980) for co-occurring hylid and ranid tadpoles, and Brockelman (1969) for bufonid tadpoles.

Larval Cover

Tadpoles of the three species found along rocky streams (S. intermontanus, B. punctatus, H. arenicolor) were all observed to respond to human disturbance by seeking cover under overhanging rocks. B. punctatus tadpoles also responded on occasion by burying themselves under silt. Both behaviors were most characteristic of mature or transforming larvae. Wassersug & Sperry (1977) have documented that transforming Pseudacris triseriata are exceptionally vulnerable to predation by garter snakes (Thamnophis sirtalis), apparently because large hind- and especially forelimbs reduce swimming efficiency, while tails interfere with hopping ability.

Newly emerged B. punctatus, H. arenicolor, H. regilla and especially S. intermontanus all possess considerable tail stubs, and presumably benefit from opportunities for immediate concealment beneath objects near water. Suitable refuges provide a damp substrate (like adults, juvenile anurans

possess a permeable skin through which water is freely lost to the atmosphere), and may comprise large rocks, boards, logs or even, for want of better, dry cow dung. Primarily nocturnal species, like spadefoots and true toads, may be found massed in such protected locations for several days following metamorphosis. The occurrence of shaded, damp microsites is predicted to be especially crucial to the survival of toadlets emerging from isolated cattle troughs, which they probably cannot easily reenter.

In general, bufonid and hylid reproductive success was found to be highest in habitats having low associated populations of invertebrate predators. This was sometimes obtained by periodic dessication of the habitat (notably at cattle tanks). The same effect may also be achieved when water bodies freeze solid in the winter. Alternatively, highly compartmentalized habitats increase the probability that at least some tadpoles are segregated from predators. Examples of such habitats include semi-isolated, rocky pools; depressions along emergent, mid-stream gravel banks; cattle hoofprints fed by seepage. The occurrence of shallow, isolated waters, particularly when deeper areas are available, may also serve to segregate these species from predaceous spadefoot tadpoles, which preferentially breed (S. intermontanus) in 7-25 cm of water.

UTILITY OF TADPOLES AS GRAZERS

In an enclosure experiment designed to test the effectiveness of Rana aurora tadpoles as algal consumers, Dickman (1968) found that the standing crop of filamentous green algae was substantially reduced in the presence of tadpoles, often to 1-2 percent of the control level. These results were consistent with the observation that dense mats of filamentous algae

disappeared under natural lake conditions, coincident with the hatching and early development of large numbers of R. aurora tadpoles.

Working with a small, natural pond ecosystem near St. Louis, Missouri, Seale (1980) found that a community of ranid and hylid tadpoles was responsible for 1) significantly reducing the rate of primary production by planktonic algae, and 2) significantly reducing the percent of blue-green algae present. She concluded that tadpoles can substantially decrease the rate of eutrophication in small water bodies, both by curtailing primary production and nitrogen fixation, and also exporting nitrogen from the system via metamorphosis.

All species of tadpoles in the present study were observed to feed upon periphyton as well as floating clumps of algae. Circumstantial evidence that at least two of these species may significantly reduce the standing crop of algae was obtained at two sites. At Cottonwood Tank, algal cover (both floating and bottom) was estimated as 55 percent of the tank's surface area on 19 April. On this date, approximately 90 spadefoot tadpoles (1.0-1.5 cm) were present, feeding on both algae and bottom sediments. By 14 May, algal cover was estimated as 6 percent, with approximately 285 spadefoot tadpoles (1.4-5.0 cm) present. By 25 May, no algae was present, while the tadpole population comprised approximately 150 spadefoot tadpoles (3.8-7.7 cm), and 20 B. punctatus tadpoles (1.0-1.2 cm). Cattle use of the tank was low over this entire period, while the noon water temperature increased from 15° C. on 19 April to 26° C. on 28 May (which in turn should have promoted algal growth rates over this time).

At Grapevine Trough, a significant growth of algae on the trough bottom and walls was not observed until approximately 3 weeks after the majority of a clutch of B. punctatus tadpoles developing in the trough had metamorphosed. (Observations began soon after the tadpoles appeared). The

major tadpole food resource at this site apparently consisted of a 3 cm layer of silty, decomposed litter at the bottom: approximately 70 percent of this was consumed over the span of larval development (300-325 tadpoles).

As suggested above, the utility of tadpoles may extend to scavenging refuse as well as consuming algae. At wildlife catchments in the low desert of southwestern Arizona, water held in ground level drinkers is characteristically clean and odorless when B. punctatus tadpoles are present. In their absence, both algae and dead insects accumulate, and the water gives off a foul odor. The occurrence of tadpoles at the catchments is probably limited at least in part by the probability that adults successfully disperse to these very isolated water sources (Todd Soderquist, Arizona Game and Fish Dept., pers. comm.).

IMPACT OF BULLFROGS (RANA CATESBEIANA) AND TIGER SALAMANDERS (AMBYSTOMA TIGRINUM) ON ANURAN POPULATIONS

Bullfrogs are the largest North American frogs, surpassing 18 cm in body length (Wright & Wright, 1949). Originally restricted to the United States east of the Great Plains, they have been successfully introduced to areas throughout the West. Adult bullfrogs are highly predaceous and carnivorous, with tastes that extend to other anurans. Introduced populations are believed to have contributed, through predation and competition, to the disappearance of R. aurora from the San Joaquin Valley, California, restriction of R. boylei in this same general area to habitats not occupied by bullfrogs, and, at least in part, elimination of the Vegas Valley frog, R. pipiens fisheri (Moyle, 1973). The effect that adult bullfrogs may have on non-ranid amphibians has not been investigated. However, R. catesbeiana tadpoles have been shown to feed effectively on suspended phytoplankton over a

wider range of concentrations than either Bufo woodhousei fowleri or especially Hyla crucifer tadpoles, and may reduce this food resource under natural field conditions to levels below that which can be utilized by other species (Seale & Beckvar, 1980).

The aquatic larvae of tiger salamanders are voracious and highly effective tadpole predators (see remarks, this report, in sections on Scaphiopus and B. punctatus). Larval tiger salamanders are also highly regarded as bait for certain freshwater fishes , and are extensively seined, transported, transplanted, and marketed in the Southwest for this reason. Such practices have occasioned widespread mixing of distinctive salamander subspecies in at least Arizona (Stebbins, 1966). The practice of annually planting larvae in ponds for later harvest is also potentially detrimental to anuran populations in several ways: 1) in creating high larval salamander densities in areas of water bodies unsuitable for the maintenance of breeding populations of salamanders; 2) in at least temporarily exacerbating predator pressure in water bodies where local salamanders do breed; 3) in introducing older, larger, and hence more effectively predaceous larvae than might occur naturally at a given elevation/latitude; 4) in maintaining high larval salamander densities despite environmental fluctuations which might depress both anuran and local salamander populations.

LIVESTOCK IMPACTS ON DESERT ANURANS

Based on the results of this study, range cattle do not adversely affect larval amphibians to any significant extent. Within reasonable limits, the addition of livestock wastes to water bodies is expected to benefit tadpoles, both directly as a food source, and indirectly in promoting algal and bacterial growth. Hoofprints, once filled with water, may provide

sheltered breeding sites. While the eggs of all species breeding in shallow waters are liable to trampling, such losses were not found to be high in this study.

Heavy browsing and trampling of riparian areas is, conversely, predicted to be highly detrimental to adult populations of most if not all anurans. Some species, like H. regilla, may specifically depend on abundant, low vegetation or its functional equivalent for cover. Others may suffer more subtle negative effects, as insect biomass decreases with reduced vegetation diversity and biomass, or the spatial extent of foraging is restricted by lowered soil moisture/increasing soil temperatures.

OFF-ROAD VEHICLE IMPACTS ON DESERT ANURANS

Like livestock, off-road vehicles (ORV's) may adversely affect anuran populations by damaging vegetation which adults depend upon for cover and as a forage base for insects (their prey).

Adults and larvae are also liable to injury or death as a result of being run over. The adults of many widespread desert species (e.g. Scaphiopus sp., Bufo alvarius, B. cognatus, B. punctatus) respond to the disappearance of ephemeral surface waters by burrowing. Scaphiopus sp., and probably others, also retire to shallow burrows during the days between foraging nights. Based on data collected by Ruibal et al. (1969) in the vicinity of Portal, Arizona, buried animals may be extremely vulnerable to ORV's, particularly when ORV activity is concentrated along washes or in the vicinity of permanent or temporary surface waters: 1) Burrows are frequently shallow. The burrows of summer active S. hammondi were found to range in depth from 1.3-4.9 cm. Overwintering animals apparently dig an initially fairly shallow burrow (range of September/October depths = 8-38 cm), deepen the burrow into the winter

(range of February/March depths = 28-91 cm), and then gradually dig their way upward prior to rain-induced full emergence (range of June/July depths = 12-69 cm). Bondello & Brattstrom (1979) have demonstrated that exposure of burrowed S. couchi to recorded motorcycle sounds of "intermediate intensity" stimulates the animals to dig upward and emerge, even at an inappropriate season (October/November). The vibration apparently mimics acoustical cues provided by summer thunderstorms. 2) Burrowed S. hammondi were found concentrated, frequently in company with B. cognatus, S. couchi or S. bombifrons, in a small portion of the areas available to them. 3) Of four investigated sites, two were located along shallow (e.g. 2 m deep) ravines, while a third comprised "a flat area about 20 m from an arroyo bed." 4) All burrows occurred in open areas, and not beneath large rocks, bushes, or trees. 5) Friable, sandy, and presumably highly compactible soils were preferred. 6) Adults and juveniles were found to burrow at the same sites.

Ironically, populations occurring along the dry washes often chosen as ORV race routes are probably more susceptible to extirpation from vehicular disturbance than populations occupying more mesic areas. Inhabiting relatively unproductive and extreme habitats, such populations are predicted to be small, highly localized, and prone to breeding failure. For example, Tevis (1966) reports that breeding by B. punctatus along an ephemeral water course in southern California was either not attempted or wholly unsuccessful in four of five consecutive years. In the fifth year, approximately 30 of an estimated 34,000 eggs were able to metamorphose before the stream completely dried. A relatively long adult lifespan is apparently the key life history characteristic allowing such populations to persist. Of 17 toads marked at the beginning of the study, five were recaptured four years later, all in the original area of occurrence.

IMPACT OF SPRING DEVELOPMENTS ON DESERT ANURAN POPULATIONS

The complete diversion of surface water to distant cattle tanks or troughs will eliminate the possibility of breeding by local anurans, except (in the American West) in the case of a wholly terrestrial species, Eleutherodactylus augusti. Even reduced flows may result in smaller adult populations, if either larval success declines in consequence, or adult habitat quality diminishes. Such losses will not necessarily be offset by new populations forming around the tanks/troughs to which water has been diverted. As discussed elsewhere in this report, anuran populations may occur only where specific edaphic, vegetative, or other structural environmental criteria are met. Furthermore, the number of adults which are supported by a given expanse of riparian vegetation will almost certainly exceed the number which can be supported by the presumably xeric habitat surrounding a manmade watering site. Finally, natural dispersal of anurans to newly created waters may be problematic, both because of intrinsic problems associated with movement across arid landscapes, and the strong tendency of at least some species to return to breed at familiar sites. For example, European common toads (Bufo bufo) were found to move to a former pond for five consecutive breeding seasons after the site was drained and filled (McMillan, 1963).

LITERATURE CITED

- Ballinger, R. E., & C. O. McKinney. 1966. Developmental temperature tolerance of certain anuran species. J. Exp. Zool. 161:21-28.
- Beiswenger, R. E. 1978. Responses of Bufo tadpoles (Amphibia, Anura, Bufonidae) to laboratory gradients of temperature. J. Herp. 12:499-504.
- Black, J. H. 1974. Larval spadefoot survival. J. Herp. 8:371-373.
- Blair, A. P. 1955. Distribution, variation, and hybridization in a relict toad (Bufo microscaphus) in southwestern Utah. Amer. Mus. Novit. 1722:17-33.
- Bragg, A. N. 1941. Some observations on amphibia at and near Las Vegas, New Mexico. Great Basin Nat. 2:109-117.
- , 1945. The spadefoot toads in Oklahoma with a summary of our knowledge of the group. II. Amer. Natur. 79:52-72.
- , 1965. Gnomes of the Night. Univ. of Pa. Press, Philadelphia.
- , & C. C. Smith. 1942. Observations on the ecology and natural history of Anura. IX. Notes on breeding behavior in Oklahoma. Great Basin Nat. 3:33-50.
- Brattstrom, B., & M. Bondello. 1979. The effects of ORV sounds on the emergence of Couch's spadefoot toad, Scaphiopus couchi. Final Report, USDI Bureau of Land Management, Riverside, California.
- Brazel, A. J., J. A. Quinn, J. D. McQueen, J. A. Catalano, & T. Chico. 1981. Arizona Climate Inventory. Volume I. Final Report, USDI Bureau of Land Management, Phoenix, Arizona.
- Brockelman, W. Y. 1969. An analysis of density effects and predation in Bufo americanus tadpoles. Ecology 50:632-644.
- Brodie, E. D., Jr. & D. R. Formanowicz, Jr. 1983. Prey size preference of predators: differential vulnerability of larval anurans. Herpetologica 39:67-75.
- Brown, H. A. 1966. Embryonic temperature adaptations and genetic compatibility in two allopatric populations of the spadefoot toad, Scaphiopus hammondi. Evolution 21:742-761.
- , 1967. High temperature tolerance of the eggs of a desert anuran, Scaphiopus hammondi. Copeia 1967:365-370.
- , 1969. The heat resistance of some anuran tadpoles (Hylidae and Pelobatidae). Copeia 1969:138-147.
- Brues, C. T. 1932. Further studies on the fauna of North American hot springs. Proc. Amer. Acad. Arts and Sciences 67:184-303.

- Caldwell, P., J. H. Thorp, & T. O. Jervey. 1980. Predator-prey relationships among larval dragonflies, salamanders, and frogs. Oecologia 46:285-289.
- Calef, G. W. 1973. Natural mortality of tadpoles in a population of Rana aurora. Ecology 54:741-758.
- Creusere, F. M., & W. G. Whitford. 1976. Ecological relationships in a desert anuran community. Herpetologica 32:7-18.
- Cunningham, J. D., & D. P. Mullally. 1956. Thermal factors in the ecology of the Pacific treefrog. Herpetologica 12:68-79.
- Dickman, M. 1968. The effect of grazing by tadpoles on the structure of a periphyton community. Ecology 49:1188-1190.
- Dimmitt, M. A., & R. Ruibal. 1980. Environmental correlates of emergence in spadefoot toads (Scaphiopus). J. Herp. 14:21-29.
- Eubank, M. E., and R. C. Brough. 1979. Utah Weather. Horizon Pub., Bountiful, Utah.
- Gosner, K. L. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. Herpetologica 32:7-18.
- , & I. H. Black. 1957. The effects of acidity on the development of New Jersey frogs. Ecology 38:256-262.
- Hardy, R. 1938. An annotated list of reptiles and amphibians of Carbon County, Utah. Proc. Utah Acad. Sci. Arts and Letters 15:99-102.
- Jackman, R., S. Nowicki, D. J. Aneshansley, & T. Eisner. 1983. Predatory capture of toads by fly larvae. Science 222:515-516.
- Licht, L. E. 1968. Unpalatability and toxicity of toad eggs. Herpetologica 24:93-98.
- , 1969. Palatability of Rana and Hyla eggs. Amer. Mid. Nat. 82:296-298.
- Linsdale, J. M. 1938. Environmental responses of vertebrates in the Great Basin. Amer. Mid. Nat. 19:1-206.
- McMillan, N. F. 1963. Toads continuing to migrate for spawning to a now vanished pond. Brit. J. Herp. 3:88.
- Moyle, P. B. 1973. Effects of introduced bullfrogs, Rana catesbeiana, on the native frogs of the San Joaquin Valley, California. Copeia 1973:18-22.
- Nathan, J. M., & V. G. James. 1972. The role of protozoa in the nutrition of tadpoles. Copeia 1972:669-679.
- Noland, R., & G. R. Ultsch. 1981. The roles of temperature and dissolved oxygen in microhabitat selection by the tadpoles of a frog (Rana pipiens) and a toad (Bufo terrestris). Copeia 1981:645-652.

- Ruibal, R., L. Tevis, Jr., & V. Roig. 1969. The tenestrial ecology of the spadefoot toad, Scaphiopus hammondi. Copeia 1969:571-584.
- Schechtman, A. M., & J. B. Olson. 1941. Unusual temperature tolerance of an amphibian egg (Hyla regilla). Ecology 22:409-410.
- Seale, D. B. 1980. Influence of amphibian larvae on primary production, nutrient flux, and competition in a pond ecosystem. Ecology 61:1531-1550.
- , & N. Beckvar. 1980. The comparative ability of anuran larvae (genera: Hyla, Bufo, and Rana) to ingest suspended blue-green algae. Copeia 1980:495-503.
- Smith, H. M. 1947. On the number of eggs laid by certain species of Bufo. Science 105:619.
- Stebbins, R. C. 1951. Amphibians of Western North America. Univ. of Calif. Press, Berkeley and Los Angeles.
- , 1966. A Field Guide to Western Reptiles and Amphibians. Houghton Mifflin Co., Boston.
- Steinwascher, K. 1978. The effect of coprophagy on the growth of Rana catesbeiana tadpoles. Copeia 1978:130-134.
- , & J. Travis. 1983. Influence of food quality and quantity on early larval growth of two anurans. Copeia 1983:238-242.
- Tanner, V. M. 1939. A study of the genus Scaphiopus. Great Basin Nat. 1:3-26.
- Tevis, L., Jr. 1966. Unsuccessful breeding by desert toads (Bufo punctatus) at the limit of their ecological tolerance. Ecology 47:766-775.
- Turner, F. B. 1959. Some features of the ecology of Bufo punctatus in Death Valley, California. Ecology 40:175-182.
- Volpe, E. P. 1953. Embryonic temperature adaptations and relationships in toads. Physiol. Zool. 26:344-354.
- Voss, W. J. 1961. Rate of larval development and metamorphosis of the spadefoot toad, Scaphiopus bombifrons. Southwest Nat. 6:168-174.
- Wassersug, R. J. 1972. The mechanism of ultraplanktonic entrapment in anuran larvae. J. Morph. 137:279-288.
- , & E. A. Seibert. 1975. Behavioral responses of amphibian larvae to variation in dissolved oxygen. Copeia 1975:86-103.
- , & D. G. Sperry. 1977. The relationship of locomotion to differential predation in Pseudacris triseriata (anura: Hylidae). Ecology 58:830-839.
- Wood, W. F. 1935. Encounters with the western spadefoot, Scaphiopus hammondi, with a note on a few albino larvae. Copeia 1935:100-102.

Wright, A. H., & A. A. Wright. 1949. Handbook of Frogs and Toads of the United States and Canada. Cornell Univ. Press, Ithaca, New York.

Wylie, S. R. 1981. Effects of basking on the biology of the Canyon Treefrog, Hyla arenicolor Cope. Ph.D. Diss., Ariz. State Univ., Tempe.

Zweifel, R. G. 1961. Larval development of the Tree Frogs Hyla arenicolor and Hyla wrightorum. Amer. Mus. Novit. 2056:1-19.

----- . 1968. Reproductive biology of anurans of the arid southwest, with emphasis on adaptations of embryos to temperature. Bull. Amer. Mus. Nat. Hist. 140:1-64.

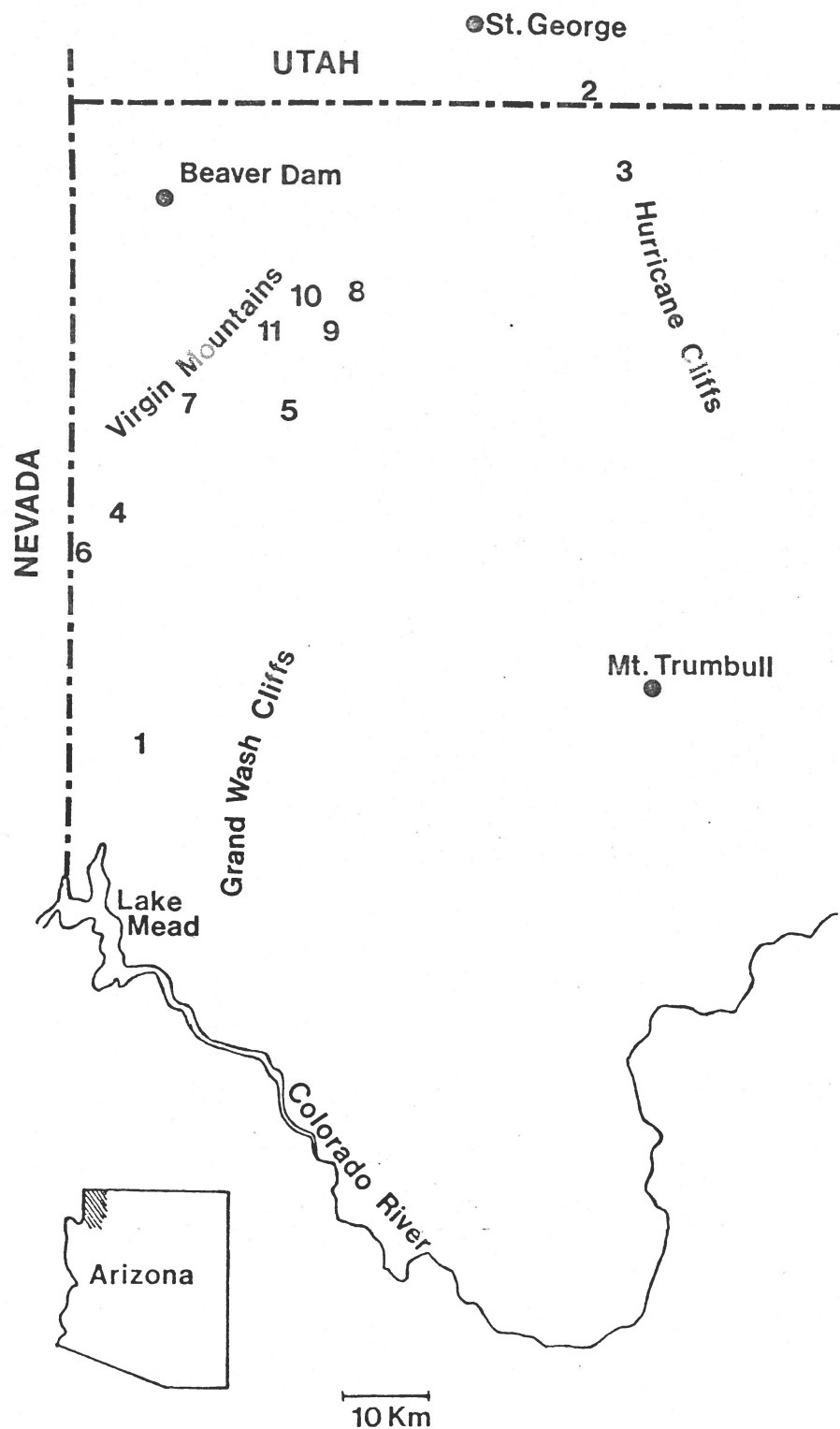


FIG. 1. STUDY SITE LOCATIONS. 1 = GRAPEVINE SPRING; 2 = FT. PIERCE WASH; 3 = COYOTE SPRING; 4 = WHITE SADDLE SPRING; 5 = SAND SPRING; 6 = MIDDLE SPRING; 7 = COTTONWOOD TANK; 8 = BLACK ROCK SPRING; 9 = MAPLE SPRING; 10 = LARSON TANK; 11 = TRAIL'S END TANK.

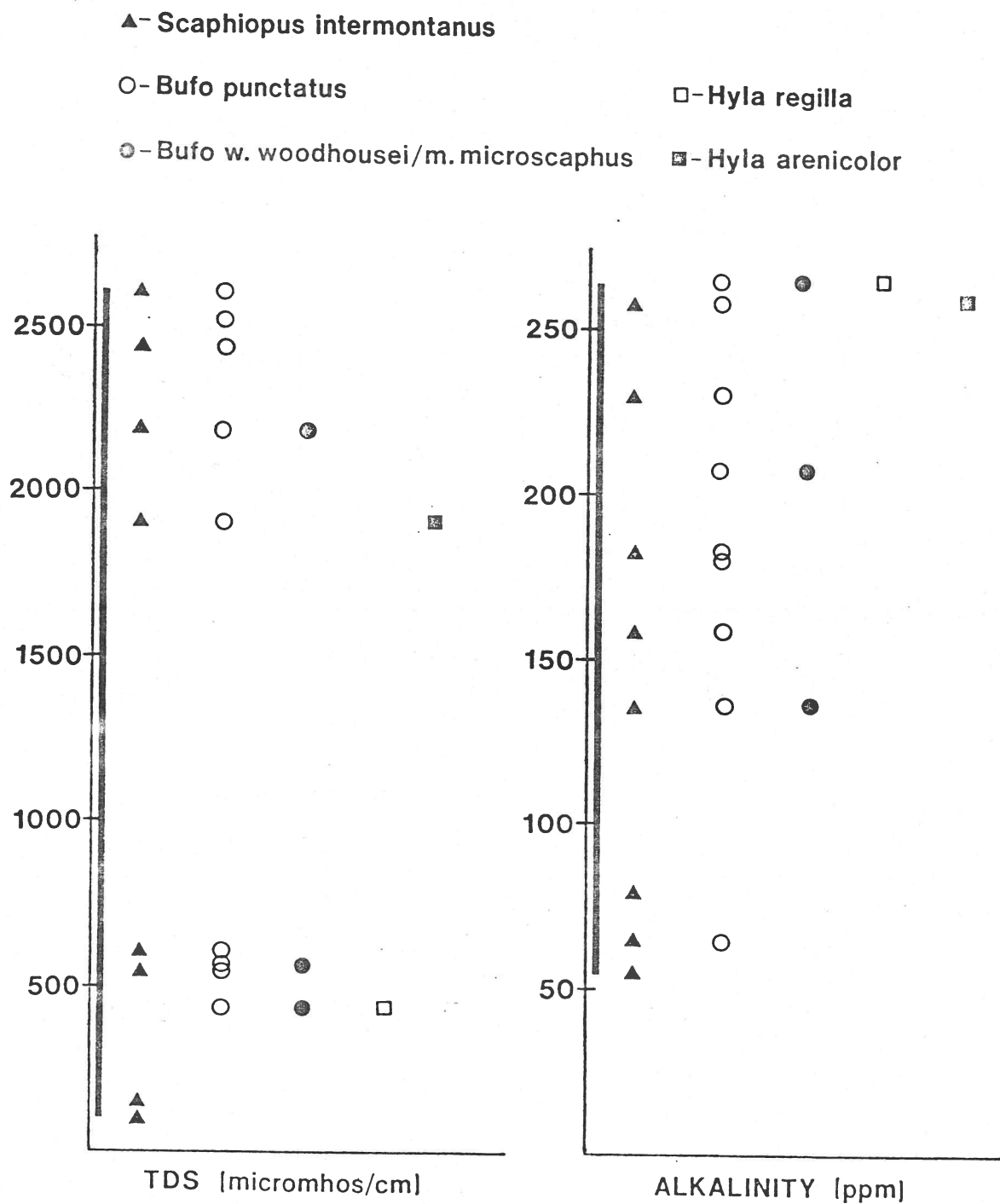


FIG. 2. ANURAN OCCURRENCE AS A FUNCTION OF MEAN TOTAL DISSOLVED SOLIDS (ESTIMATED AS CONDUCTANCE) AND ALKALINITY AT STUDY SITES (STREAMS AND TANKS).

Table 1. Study site locations (state, legal description).

SITE	STATE	LEGAL DESCRIPTION				
Grapevine Spring	AZ	T34N	R16W	Sec. 23	SW1/4	SE1/4
Ft. Pierce Wash	UT	T43S	R14W	Sec. 34	S1/2	NE1/4
Coyote Spring (Tank)	AZ	T41N	R10W	Sec. 22	NE1/4	SW1/4
White Saddle Spring (Tank)	AZ	T37N	R16W	Sec. 34	NW1/4	NW1/4
Sand Spring	AZ	T38N	R14W	Sec. 14	NW1/4	SE1/4
Middle Spring	AZ	T36N	R16W	Sec. 7	S1/2	SE1/4
Cottonwood Tank	AZ	T38N	R15W	Sec. 10	NW1/4	SW1/4
Black Rock Spring (Tanks)	AZ	T39N	R13W	Sec. 5	NE1/4	SE1/4
Maple Spring	AZ	T39N	R13W	Sec. 17	S1/2	SW1/4
Larson Tank	AZ	T39N	R14W	Sec. 1	NE1/4	SE1/4
Trail's End Tank	AZ	T39N	R14W	Sec. 21	SE1/4	NE1/4

Table 2. Anuran occurrence as a function of elevation.

SITE	SPECIES*					ELEVATION (M)
	A	B	C	D	E	
Grapevine		X	X			520
Ft. Pierce	X	X	X			895
Coyote	X	X				1045
White Saddle		X				1150
Sand	X	X				1290
Middle		X	X	X		1295
Cottonwood	X	X				1435
Black Rock	X	X				1535
Maple	X	X			X	1660
Larson	X					2080
Trail's End	X					2145

*A = Scaphiopus intermontanus,

B = Bufo punctatus,

C = B. w. woodhousei/B. m. microscaphus

D = Hyla regilla,

E = H. arenicolor.

Table 3. Physical characteristics of Scaphiopus intermontanus egg placement sites.

SITE	NO. OF CLUTCHES	EGG DEPTH (cm)	WATER DEPTH (cm)	DIST. FROM SHORE (cm)	ATTACHMENT SUBSTRATE	WATER FLOW RATE
Ft. Pierce	3	4-12	4-12	8-100	silt; gravel	slow
Sand	3	3-10	6-10	20-40	rock; gravel; bottom litter; floating algae	slow-moderate
Squaw Pockets (potholes)	1	5-20	5-20	10-50	gravel; small rocks	none
Cottonwood	3	2-20	6-25	30-100	live grass stems; floating litter	none
Black Rock	3	0.5-20	7-31	15-130	live plant stems	negligible
Maple	1	4-11	4-13	80-100	rocks; dead twigs/leaves	very slow
Lone Pine (tank)	2	1-10	7-20	45-200	live grass stems; anchored litter	none
Trail's End	1	0.3-10	10-25	50-200	dead twigs	none

Table 4. Extreme dates of Scaphiopus intermontanus reproduction, 1983.

SITE	FIRST OVIPOSITION	LAST OVIPOSITION	LAST TADPOLE OCCURRENCE
Ft. Pierce	12 March	02 May	29 July
Coyote	25 March	14 June	16 July
Sand	17 April	21 May	18 July
Cottonwood	06 April	03 August	>12 October
Black Rock	03 April	19 July	25 August
Maple	11 May	08 June	08 August
Larson	09 May	18 August	>08 October
Trail's End	14 May	24 May	20 July

Table 5. Temporal distribution of Scaphiopus intermontanus reproduction, 1983.

SITE	NO. OF CLUTCHES					
	MARCH	APRIL	MAY	JUNE	JULY	AUGUST
Ft. Pierce	*	*	1	0	0	0
Coyote	1	2-3	0	1	0	0
Sand	0	*	*	0	0	0
Cottonwood	0	5	0	0	0	1
Black Rock	0	1	2	1	1	0
Maple	0	0	2	1	0	0
Larson	0	0	*	0	0	1
Trail's End	0	0	*	0	0	0

*Several to many, exact number unknown.

Table 6. Physical characteristics of Bufo punctatus egg placement sites.

SITE	NO. OF CLUTCHES	WATER DEPTH (cm)	DISTANCE FROM SHORE (cm)	ATTACHMENT SUBSTRATE	WATER FLOW RATE
Grapevine	6	0.5-5	0-30	leaf litter; silt; matted living plants	none-slow
Ft. Pierce	10 or more	1-6	0-90	silty sand/gravel	negligible-moderate
Coyote	2	2-3	0-70	silt	none-very slow
White Saddle	5	2-8.5	4-60	fine sand	negligible-slow
Sand	3	2-6.5	3-90	sand; sandy gravel	slow-moderate
Middle	3	0.3-5	0-35	silt; fine sand	none-moderate
Black Rock	4	2-4	0-40	silt; silty litter	negligible-moderate
Maple	2	1-3	0-30	sand; sandy gravel	slow

Table 7. Bufo punctatus egg and early larval* temperature microhabitats.

SITE	DATE	TEMP. AT EGGS (°C)	EGG DEPTH/ DIST. FROM SHORE (cm)	TEMP. AT LARVAE (°C)	LARVAL DEPTH/ DIST. FROM SHORE (cm)	CONTROL TEMP (°C)	DEPTH/DIST. FROM SHORE (cm)
Grapevine	24 April	21	3/10			21	M.C.**
Grapevine	24 April	21	2.5/8			21	M.C.
Grapevine	24 April			21	0.5/4	21	M.C.
Ft. Pierce	04 May	24.5	4/20			24	M.C.
Ft. Pierce	04 May	25	1.5/15			24	M.C.
Ft. Pierce	04 May	25	1/15			24	M.C.
Ft. Pierce	04 May	24	1.5/15			24	M.C.
Ft. Pierce	04 May			25.5	2/20	24	M.C.
White Saddle	06 May	23	1.5/20			20	8/40
Ft. Pierce	12 May			24	2/10	22.5	M.C.
Ft. Pierce	12 May			26.5	1.5/10	22.5	M.C.
Middle	14 May			17.5	4/6	16	M.C.
White Saddle	14 May			23	1.5/8	20	8/35
Ft. Pierce	18 May	24.5	2/2			24.5	M.C.
Grapevine	19 May	20	1/10			20	M.C.
Middle	25 May			31	2/5	20.5	M.C.
White Saddle	28 May	32.5	3.5/15			29.5	8/40
Grapevine	11 June			22	2/10	22	M.C.
Grapevine	11 June			24	2/5	24	M.C.
Ft. Pierce	14 June			30.5	2.5/20	29	M.C.
Ft. Pierce	14 June			29	3/120	29	M.C.
Black Rock	15 June	18	2/20			16	8/35
Black Rock	15 June	23	3/10			22	8/40
Sand	18 June	29.5	1.5/10			30	M.C.
Sand	18 June			29.5	3/10	29.5	M.C.
Ft. Pierce	29 June	27	3/6			22	M.C.
Grapevine	10 July	28	2.5/10			22	M.C.
Ft. Pierce	28 July	29	4/160			29	M.C.
White Saddle	02 August	29	3/25			26	8/40
Grapevine	09 August	27.5	0.5/3			25	M.C.
Coyote	10 August	26.5	2/30			22.5	8/40
Ft. Pierce	24 August			20.5	2.5/20	19	M.C.

* ♂ Gosner Stage 20

**M.C. = Main Current

Table 8. Extreme dates of Bufo punctatus reproduction, 1983.

SITE	FIRST OVIPOSITION	LAST OVIPOSITION	LAST TADPOLE OCCURRENCE
Grapevine	20 April	17 August	10 September
Ft. Pierce	22 April	22 August	22 September
Coyote	18 May	08 August	07 September
White Saddle	07 May	17 August	26 September
Sand	20 May	19 August	18 September
Middle	14 May	31 July	02 October
Cottonwood	16 May	02 August	09 October
Black Rock	19 May	22 July	24 August
Maple	19 May	08 July	21 July

Table 9. Temporal distribution of Bufo punctatus reproduction, 1983.

SITE	NO. OF CLUTCHES				
	APRIL	MAY	JUNE	JULY	AUGUST
Grapevine	3	5	3	2	2
Ft. Pierce	*	*	2	2	1
Coyote	0	1	1	2	1
White Saddle	0	3	2	1	2
Sand	0	2	3	1	1
Middle	0	3	0	2	2
Cottonwood	0	1	0	1	2
Black Rock	0	1	6	2	0
Maple	0	2	2	1	0

*Several to many, exact number unknown.

Table 10. Physical characteristics of Bufo w. woodhousei/B. m. microscaphus, Hyla regilla, and H. arenicolor egg placement sites.

SITE	NO. OF CLUTCHES	WATER DEPTH (cm)	DISTANCE FROM SHORE (cm)	ATTACHMENT SUBSTRATE	WATER FLOW RATE
<u>Bufo w. woodhousei</u> / <u>B. m. microscaphus</u>					
Grapevine	1	1.5-4	5-20	leaf litter	slow
Ft. Pierce	3-4	0-8	15-110	silty sand/ gravel; rock	slow-fast
Lower Beaver Dam Wash	1	3-10	5-30	fine gravel	moderate
<u>Hyla regilla</u>					
Middle	12 or more	0-7	5-105	silt; attached, in water column, to stems, algae	none- moderate
<u>H. arenicolor</u>					
Gates-Mullen (spring-fed stream)	2	2-8	15-30	silty sand	slow
Maple	3	2.5-10	5-30	silt, sand, gravel	slow

Table 11. Bufo w. woodhousei/B. m. microscaphus, Hyla regilla, and H. arenicolor egg temperature microhabitats.

SITE	DATE	TEMP. AT EGGS (°C)	EGG DEPTH/DIST. FROM SHORE (°C)	CONTROL TEMP. (°C)	DEPTH/DIST. FROM SHORE (cm)
<u>B. w. woodhousei</u> / <u>B. m. microscaphus</u>					
Ft. Pierce	23 April	20	3/50	20	M.C.*
Ft. Pierce	23 April	20	3/35	20	M.C.
Grapevine	24 April	21	3/10	21	M.C.
Ft. Pierce	04 May	24	3/40	24	M.C.
<u>H. regilla</u>					
Middle	01 May	18	6/5	16	M.C.
Middle	14 May	18	1/8	17	M.C., 1/60
Middle	14 May	21	1/12	19	8/20
Middle	25 May	21.5	6.5/8	20.5	M.C.
<u>H. arenicolor</u>					
Maple	03 May	16.5	6/20	12.5	8/25
Gates-Mullen	07 May	24	2/8	21	8/25
Maple	17 May	14.5	3/20	12	M.C.
Maple	17 May	13.5	2.5/10	12	M.C.
Maple	17 May	14.0	5/20	12	M.C.

*Main Current

Appendix 1. Total dissolved solids concentrations. Reported, indirectly, as specific conductance, in micromhos/cm.

SITE	DATE										MEAN	STD. DEV.
	1-15 MAY	16-31 MAY	1-15 JUNE	16-30 JUNE	1-15 JULY	16-31 JULY	1-15 AUG.	16-31 AUG.	1-15 SEPT	16-31 SEPT		
Grapevine	435	460	520	585	610	575	596	595	610	615	560	62
Ft. Pierce	2080	2150	2400	2600	2400	2240	1650	2050	2360	2000	2193	255
Coyote (Tank)	2100	2300	2800	4000	3000	3000	1620	1800	2200	1740	2456	704
Coyote (Trough)	2000	2000	2000	2300	2220	2200	2080	2210	2200	2150	2136	103
White Saddle	2140	2200	2350	2590	2600	2850	2540	2600	2600	2700	2517	210
Sand	----	2260	2350	2590	2900	2850	2700	2790	2290	2750	2609	234
Middle	420	440	385	408	418	455	425	445	450	445	429	21
Cottonwood	210	275	415	510	660	805	860	715	520	295	526	217
Black Rock	465	505	560	610	690	605	730	700	725	385	597	112
Maple	1620	1700	1970	2200	1900	1990	1990	1990	2000	1670	1903	173
Larson	----	130	130	130	138	133	225	119	152	102	140	33
Trail's End	----	82	88	81	98	83	75	90	103	99	89	9

Appendix 2. Midmonth nitrate/nitrite concentrations (mg/liter).

SITE	MONTH					MEAN	STD DEV
	MAY	JUNE	JULY	AUGUST	SEPT		
Grapevine	.012	.014	.018	.016	.027	.017	.005
Ft. Pierce	.011	.015	.015	.015	.012	.014	.002
Coyote (Tank)	.045	.105	.050	.042	.023	.053	.028
Coyote (Trough)	.018	.005	.023	.032	.009	.017	.010
White Saddle	.018	.017	.003	.024	.008	.014	.008
Sand	.015	.036	.015	.018	.002	.017	.011
Middle	.405	.488	.495	.435	.360	.437	.051
Cottonwood	.015	.053	.068	.024	.019	.036	.021
Black Rock	.019	.023	.003	.015	.015	.015	.007
Maple	.021	.030	.015	.011	.005	.016	.009
Larson	.021	.030	.075	.048	.010	.037	.023
Trail's End	.025	.042	.032	.029	.039	.033	.006

Appendix 3. Midmonth orthophosphate concentrations (ppm).

SITE	MONTH					MEAN	STD DEV
	MAY	JUNE	JULY	AUGUST	SEPT		
Grapevine	.02	.035	.02	.03	.025	.026	.006
Ft. Pierce	.02	.02	.035	.13	.02	.045	.043
Coyote (Tank)	.02	.02	.05	.07	.11	.054	.034
Coyote (Trough)	.04	.02	.41	.01	1.3	.356	.495
White Saddle	.02	.04	.025	.02	.015	.024	.009
Sand	.035	.03	.03	.065	.045	.041	.013
Middle	.03	.025	.05	.065	.015	.037	.018
Cottonwood	.06	.07	.03	.07	.23	.092	.071
Black Rock	.02	.02	.02	.02	.07	.030	.020
Maple	.02	.04	.03	.01	.02	.024	.010
Larson	.03	.03	.04	.04	.03	.034	.005
Trail's End	.03	.025	.04	.04	.025	.032	.007

Appendix 4. Midmonth alkalinity levels (ppm).

SITE	MONTH					MEAN	STD DEV
	MAY	JUNE	JULY	AUGUST	SEPT		
Grapevine	180	207	210	220	220	207	15
Ft. Pierce	125	135	140	155	120	135	12
Coyote (Tank)	55	45;10*	70	90	65	67	13
Coyote (Trough)	190	140	160	210	190	178	25
White Saddle	155	170	170	180	230	181	26
Sand	170	135	90	190	205	158	41
Middle	260	265	265	270	260	264	4
Cottonwood	241	370	215	195	130	230	79
Black Rock	190	190	180	203	150	183	18
Maple	250	230	250	300	260	258	23
Larson	71;2*	85;10*	100	65	60	79	16
Trail's End	37;10*	10;40*	20;40*	60	60	55	6

* = Carbonate Alkalinity
no * = Bicarbonate Alkalinity

Appendix 5. Midday (1130-1230 hours) water temperatures (°C).

SITE	DATE											MEAN	STD. DEV.
	16-30 APRIL	1-15 MAY	16-31 MAY	1-15 JUNE	16-30 JUNE	1-15 JULY	16-31 JULY	1-15 AUG.	16-31 AUG.	1-15 SEPT	16-30 SEPT	MAY- SEPT	
Grapevine	21	20	20	21.5	21	20	25	25	25	20	21	21.9	2.1
Ft. Pierce	21	23	24	28	27	26.5	28	27	27	25	18.5	25.4	2.8
Coyote (Tank)	16	17.5	19	23.5	26	29	27	27	22.5	24	18	23.3	3.9
Coyote (Trough)	13	15	16.5	21.5	24	25	24.5	24	21	22	18	21.1	3.4
White Saddle	16.5	18	29	26	22	28	27.5	29	24	23.5	22	24.9	3.4
Sand	--	22	25	24	29	25.5	25.5	28	25	26	18	24.8	2.9
Middle	19	18.5	20	19	20	20.5	20	20	19.5	20	18	19.5	0.8
Cottonwood	15	18	26	26.5	26	28	25.5	31	30	26	16.5	25.3	4.4
Black Rock	15	16	19	20	21	24	23	23	20.5	20	15	20.1	2.8
Maple	11.5	13	15.5	19	22	26	23.5	23	20	21	14	19.7	4.1
Larson	--	15	21	22	23	22	24	25	21	20	17	21.0	2.9
Trail's End	--	14	22	20	24	23	23	22	19	20	17	20.4	2.9