

# ECOLOGICAL RELATIONSHIPS IN A DESERT ANURAN COMMUNITY

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**ABSTRACT:** The surface activity and distribution patterns of five species of anurans inhabiting a watershed in the Chihuahuan Desert were studied from 1970–1974. Adult toads *Bufo debilis*, *Bufo cognatus*, *Scaphiopus hammondi*, *Scaphiopus bombifrons* and *Scaphiopus couchi* exhibited short periods of activity immediately following rain events. Juveniles of these species were active for as long as 55 days in the bottom of the ephemeral lake where vegetative cover and fissures in the clay-silt soil provided shelter and modified the microclimate due to reduced evaporation. Less than 1% of the juveniles of *S. bombifrons*, *S. hammondi* and *B. debilis* survived to adult size. The importance of spatial separation within the flooded playa during breeding and possible character displacement of breeding calls are documented and their importance in maintaining this desert anuran community is discussed.

In the Chihuahuan Desert summer rains stimulate surface activity of anurans, *Scaphiopus* sp. and *Bufo* sp. which breed in ephemeral pools (Ruibal et al., 1969). Within a few weeks after egg deposition, newly metamorphosed anurans emerge from the rapidly drying breeding sites. In late September when convectional rains of the Chihuahuan Desert summer cease, juvenile anurans must seek shelter from the cold desiccating conditions of the desert winter. Several desert anurans overwinter in underground burrows which they excavate (Bragg, 1965; McClanahan, 1967; Ruibal et al., 1969; pers. observ.).

Numerous aspects of the ecology and physiology of adult desert anurans have been reported (Brenner, 1969; Mayhew, 1962, 1965, 1968; Seymour, 1973; and Whitford, 1969). However, there is little information on the ecology of newly metamorphosed desert anurans.

This paper reports investigations of the activity and breeding biology of five species of Chihuahuan Desert anurans with emphasis on the biology of the recently metamorphosed to subadult stages in the life cycles of these species.

## SITE AND CLIMATE DESCRIPTION

This study was conducted on the Jornada Validation Site, US/IBP located on the northern edge of the Doña Ana Mountains in the Chihuahuan Desert 40 km NNE of

Las Cruces, Doña Ana County, New Mexico. The study area encompassed part of the Doña Ana Mountains, alluvial fan outwash areas (bajadas) which drain into a 12-ha ephemeral lake (playa) (Fig. 1). The playa has been subjected to little human alteration with the exception of an excavation serving as a cattle watering tank which occupies < 5% of the playa surface area. Cattle grazing was excluded from the playa and its environs from 1972.

The slope varies from 10% on the bajada to < 2% on the fringes of the playa. The soils vary from coarse gravels on the bajada to sandy-loams on the playa fringe and heavy clay silts on the playa bottom. After rains the bajada soils dry quickly due to runoff and evaporation. The clay-silt soils of the playa bottom exhibit swelling when wet and "seal" with the first rains which usually occur in late June or early July. After these soils swell, runoff from heavy rains can result in flooding. Flooding normally occurs during July and August at a frequency of once in two to three years.

Following flooding, there is little percolation into the soil but high rates of evaporation rapidly reduce the flooded area. As the playa soils dry, they shrink and crack with some fissures up to 0.5 m deep and 1–6 cm wide at the surface.

Seventy-five percent of the annual rainfall (50 year average = 211.3 mm) occurs

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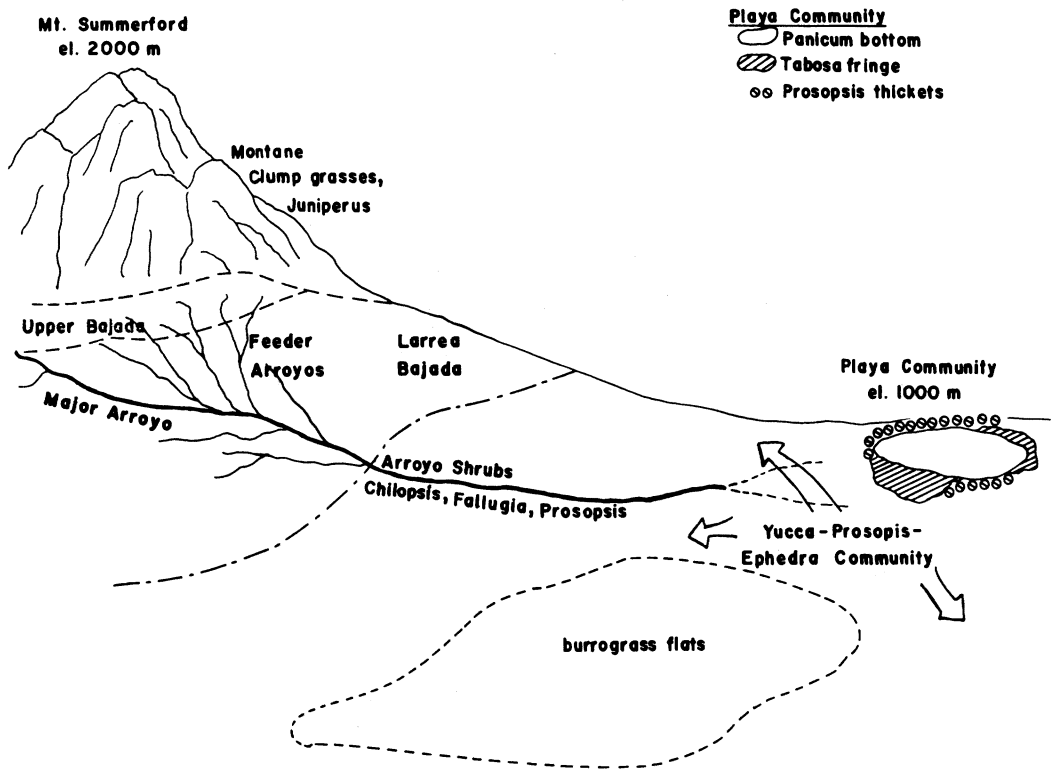


FIG. 1.—Physiography and plant communities of the Chihuahuan Desert Jornada Validation Site, US/IBP.

from May through October as convectional storms. Temperatures  $> 38^{\circ}\text{C}$  occur from mid-May through August. June is usually the hottest and driest month with infrequent storms. During winter the daily maxima usually exceed freezing on the playa. Nighttime temperatures can fall to  $-14^{\circ}\text{C}$  during winter (December through February). During the day in June and July, relative humidity may remain below 20% for several successive days. Nighttime humidities usually approach 100% because the playa acts as a cool air sink. From June through August the average nighttime relative humidity at the playa weather station is around 80%.

#### MATERIALS AND METHODS

Juvenile and adult toads were censused by hand capture and pitfall traps. The

nearly circular playa was divided into four equal quarters and a pitfall trap grid located at random in each quarter. Each grid consisted of five rows of traps, 10 traps per row with 15 m trap spacing. Daily census was made from late April through October. All toads were removed from the traps within 2 hours after sunrise to prevent death and weight loss due to desiccation. Each toad was weighed after the bladder water had been removed and snout-vent length recorded.

During the first year, 1972, juvenile toads were marked by removing a specified toe each week. Using this system juveniles marked previous weeks could be assigned to the period initially captured. Density estimates were calculated by the Lincoln Index using week one as precensus and week two as census. In subsequent years

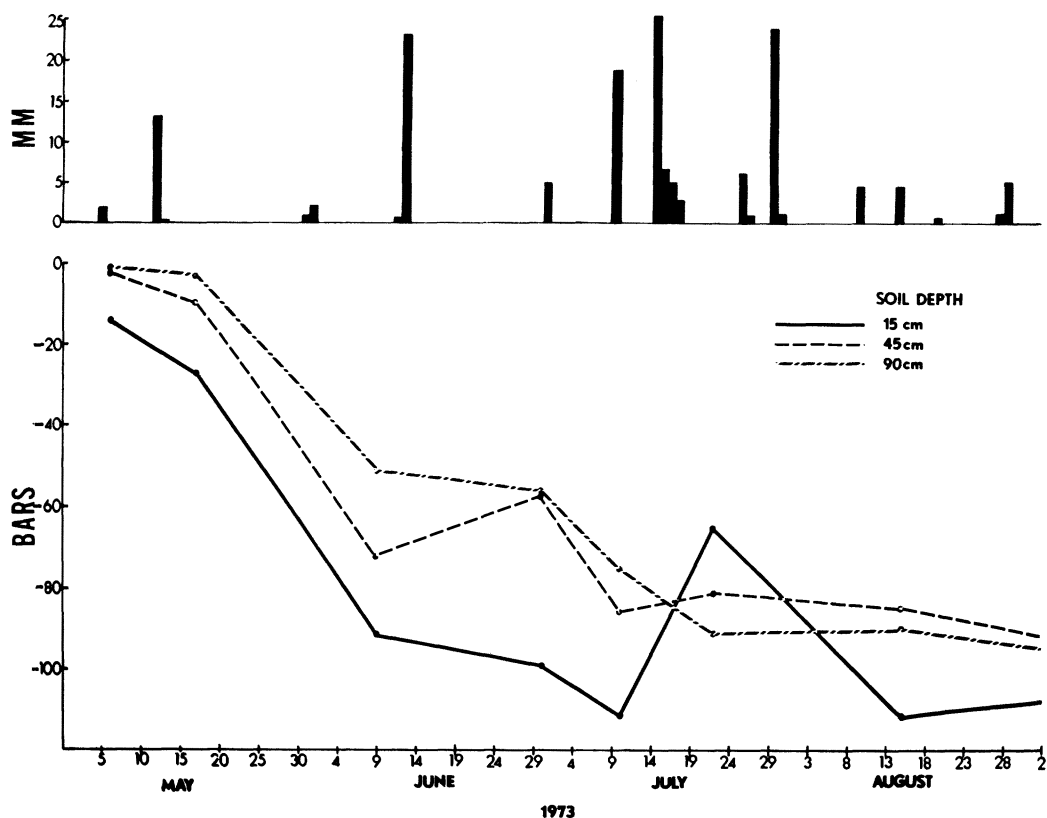


FIG. 2.—Relationship between total rainfall (mm) and soil water potential (bars) of playa soils during the summer months of 1973.

each individual was marked by a unique toe clip removing up to two toes per foot. We were able to obtain estimates of over-winter survivorship because we could recognize individuals that had been marked in previous years.

Visual census of active toads was made after rains by surveying a 25-m radius circle at 100-m intervals on random lines radiating from the playa bottom.

During breeding, adult toads were hand captured as encountered in a 3-ha section of the flooded playa and from seven rocky pools near the Doña Ana Mountains. Toads were sampled each night until activity of all species ceased. Each individual was marked by toe removal, weighed and released in the sampling grid. Toads were permitted to pursue breeding activity in

the grid for 1 hour to permit readjustment of their activity and were again captured by hand as encountered and the number of adults breeding that night estimated by the Lincoln Index, with those initially captured and released as a precensus and those captured after an hour's wait, as the census.

Habitat preference of breeding adults was determined by random transects across the flooded playa. Slow and deliberate movement did not disturb adults and permitted notation of species and habitat. Bragg (1965) also noted that toads overcame their initial fear of human presence and soon continued mating after being disturbed.

Daily rainfall amounts and intensity, air temperature, and humidity was recorded at a standard weather station on the site.

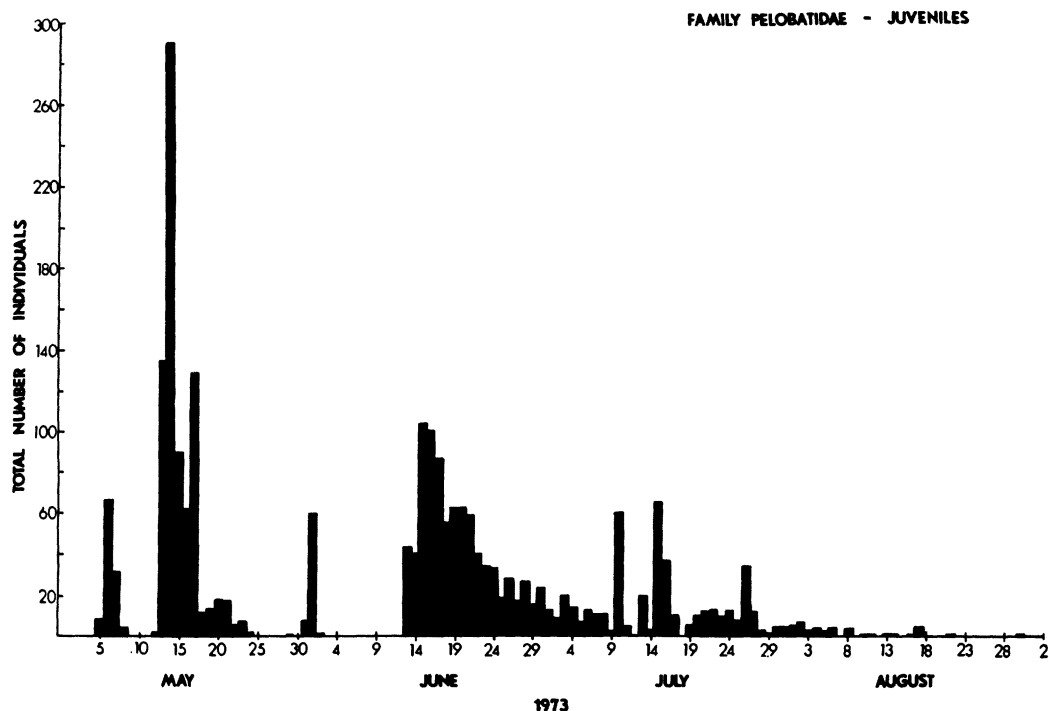


FIG. 3.—Total numbers of juvenile pelobatids active on the playa bottom from May through September 1973.

Gypsum soil blocks buried in a grid on the playa were used for soil moisture measurements at depths of 15, 30 and 45 cm. Since soil blocks were read at biweekly intervals and exhibit lags in response, the soil moisture data did not always reflect increases in moisture content immediately after rain events.

Toad calls were recorded at isolated pools near the playa using a Panasonic™ cassette tape recorder. A minimum of 20 calls per species were recorded on 1 August 1974 at temperatures ranging from 18–20°C. Calls were analyzed on a sound spectrograph (Kay Sona-Graph™ Model 6061-A). Spectrographs covered a frequency range of 8000 Hz.

### RESULTS

The activity and distribution patterns of both adult and juvenile toads were influenced by rainfall events and soil character-

istics. Patterns of rainfall and soil drying are shown in Fig. 2. Juvenile toads of all species, except *S. couchi*, tended to remain on or near the playa bottom. Juveniles of this species were seldom encountered and no conclusions could be drawn from the data. Adults of all species were found in a variety of habitats, ranging from the dense cover of the playa bottom grassland to the open bajada creosote community.

Daily toad activity, rainfall patterns, and soil drying trends on the playa are shown in Figs. 2–5. Figure 6 summarizes data on the survivorship of juvenile toads between metamorphosis and adult size. The activity of all size classes of toads was initiated by rain, with peak activity occurring within a few hours of a rainfall event. Activity steadily declined until the upper 20 cm of soil became too dry for surface activity. Juvenile toads remained inactive until subsequent rains increased soil moisture.

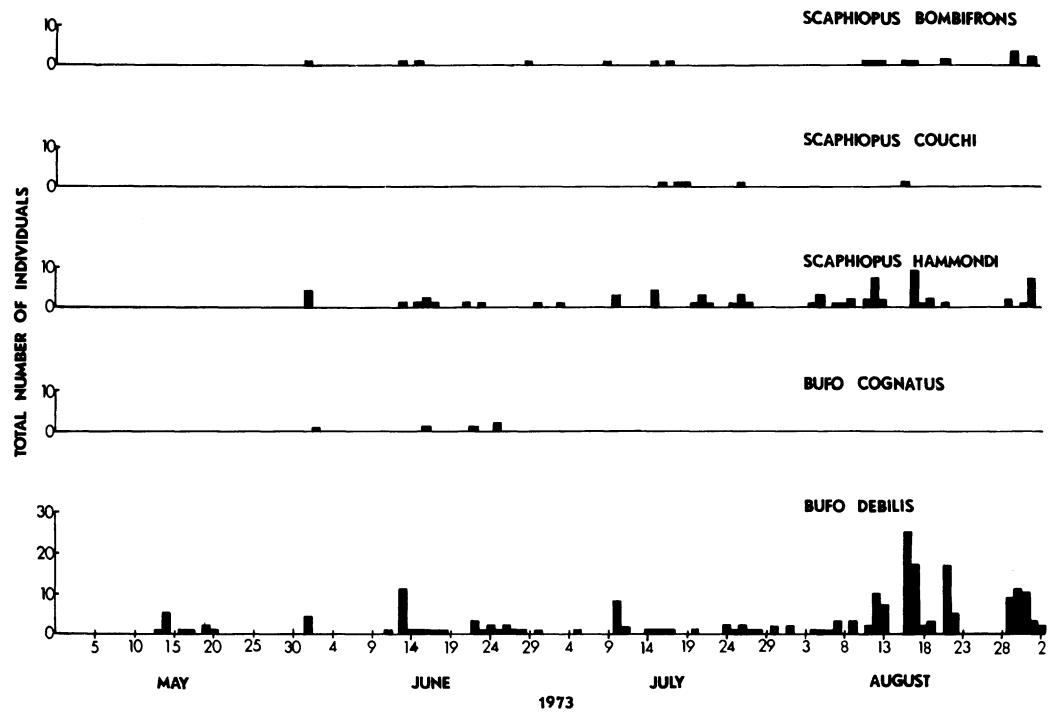


FIG. 4.—Total numbers of active adult anurans on the playa and surrounding study area from May through September 1973.

Juveniles were active for longer periods than were adults. Juvenile *S. bombifrons* and *S. hammondi* maintained activity for 55 days when rain occurred with sufficient frequency to keep soil moisture high (Figs. 2 and 3). The activity of adults of all

species occurred in spurts of short duration following rains. Cold weather or drought curtailed the activity of all age groups.

All age classes were active at night, except on rare occasions when dense overcast resulted in diurnal activity. This in-

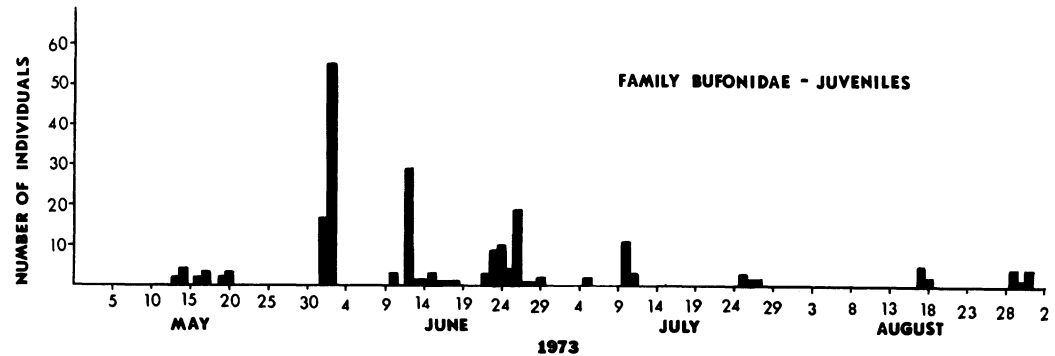


FIG. 5.—Total numbers of juvenile bufonids active on the playa bottom from May through September 1973.

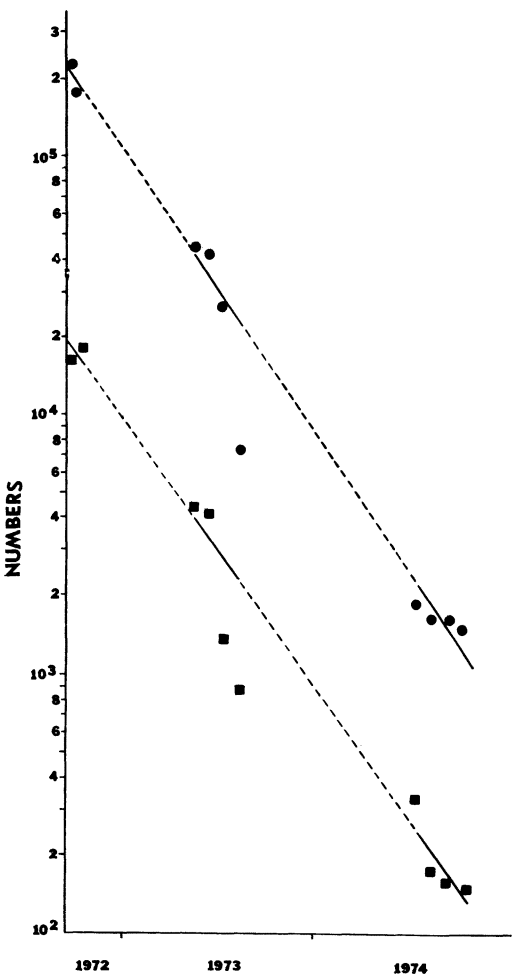


FIG. 6.—Estimated numbers of pelobatids and bufonid juveniles (which metamorphosed in 1973) surviving in 1973 and 1974. Circles are data for pelobatids; the squares, bufonids. Dotted lines represent the overwinter hibernation period when no population estimates could be made.

frequent daytime activity was related to increased humidity and lower temperature.

During one 6-week period, when one of us (F.M.C.) was on the playa from sunrise to sunset, the daily behavior of juvenile toads began to retreat under surface objects (old cow dung, wood, clumps of dead vegetation) or into fissures. About 1 h before sunset they began to emerge. Examination of surface objects under which the juveniles had retreated in the morning revealed numbers of dead animals. Not all the juveniles that sought shelter under surface objects died. A conservative estimate is that about one-half died. When hardened clay (10–15 cm thick) around fissures was removed all of the toads were alive.

Isolating mechanisms were documented in adults. Isolating mechanisms included call and habitat selection of breeding adults. Habitat preference and incidence of amplexus of breeding adults are shown in Tables 1 and 2. Calls of adult breeding males are shown in Fig. 7. All had distinctive calls. There was some evidence of habitat preference differences in nonbreeding adults (Table 3). The smaller species, *B. debilis* ( $\bar{x}$  weight = 7.2 g,  $N > 100$ ), *S. bombifrons* ( $\bar{x}$  weight = 17.9 g,  $N > 100$ ), and *S. hammondi* ( $\bar{x}$  weight = 11.4 g,  $N > 100$ ), were generally found on or near the playa, whereas the larger species, *B. cognatus* ( $\bar{x}$  weight = 62.7 g,  $N = 68$ ) and *S. couchi* ( $\bar{x}$  weight = 36.3,  $N > 100$ ), preferred habitat more distant from the playa.

TABLE 1.—Occurrence of breeding adults of five species of Chihuahuan Desert anurans in a variety of habitats in a playa lake. Water depths < 12 cm are indicated by <, those > 12 cm by >. Numbers are actual numbers recorded in a given habitat.

Habitat	Scaphiopus bombifrons		Scaphiopus couchi		Scaphiopus hammondi		Bufo cognatus		Bufo debilis	
	<	>	<	>	<	>	<	>	<	>
open water	3	12	1	0	29	297	1	5	3	9
sparse vegetation	16	167	3	0	7	29	0	39	62	40
dense vegetation	0	0	133	2	1	0	17	22	11	30
other	1	3	5	0	6	1	1	1	2	3

TABLE 2.—The incidence of intra- and interspecific amplexus in five sympatrically breeding anurans in a Chihuahuan Desert playa lake.

	<i>Scaphiopus bombifrons</i>	<i>Scaphiopus couchi</i>	<i>Scaphiopus hammondi</i>	<i>Bufo cognatus</i>	<i>Bufo debilis</i>
<i>S. bombifrons</i>	143	2	57	0	0
<i>S. couchi</i>		61	0	0	0
<i>S. hammondi</i>			211	0	0
<i>B. cognatus</i>				36	0
<i>B. debilis</i>					69

All species, except *S. bombifrons* and *S. hammondi*, were reproductively segregated during amplexus. The incidence of amplexus between *S. bombifrons* and *S. hammondi* was 16.1%. We could not determine what percent of these interspecific amplexing pairs produced viable offspring.

All species reproduced when the playa flooded in 1970, 1972 and 1974. The playa failed to flood in 1971 and 1973, although the cattle tank filled partially in June 1973, permitting  $\approx$  1000 pelobatids to reproduce successfully. The bufonid species did not breed on our site in 1973. The playa normally remained flooded for a period of about 6 weeks, but several heavy rains in the fall of 1972 kept the playa flooded until November. In 1973, the cattle tank remained flooded for only 3 weeks, but most of the tadpoles metamorphosed before the tank dried.

Figure 8 shows the relative densities and duration of stay of breeding adults in the cattle tank in 1973 and the flooded playa in 1974. The pelobatids comprised 93% of the breeding adult population at maximum densities in 1974 and all of the breeding population in the cattle tank in 1973. The duration of breeding activity was brief for *B. cognatus* and *S. couchi* at the playa site, whereas *B. debilis*, *S. bombifrons* and *S. hammondi* remained at the flooded playa for longer periods.

Adults of each species exhibited preferences for breeding habitat (Table 1). Three species, *B. cognatus*, *B. debilis* and *S. couchi*, preferred grass clump habitats in the playa. Two species, *S. bombifrons* and *S. hammondi*, preferred open, deep-

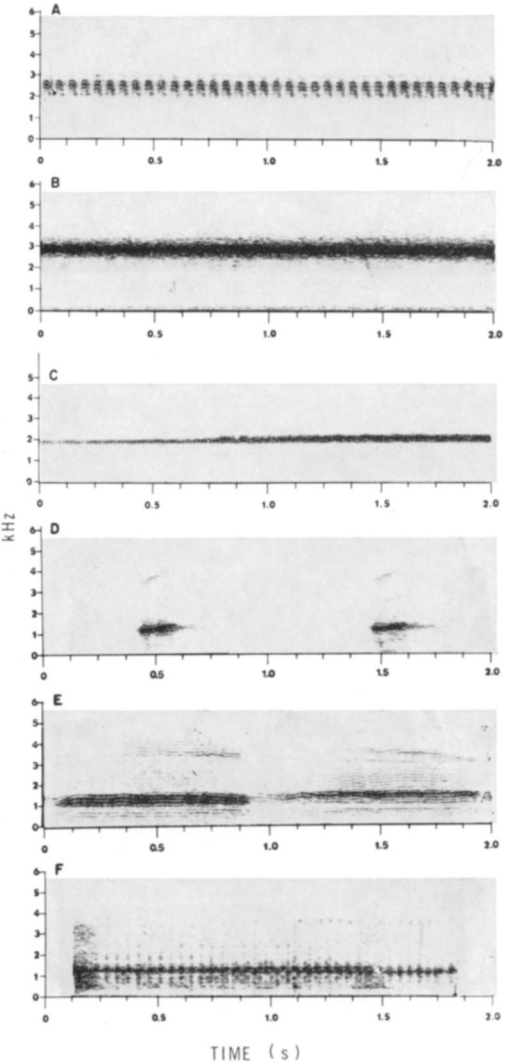


FIG. 7.—Sonograph records of the calls of anurans breeding at the Jornada playa. (A) *Bufo cognatus*; (B) *B. debilis*; (C) *B. punctatus*; (D) *Scaphiopus bombifrons*; (E) *S. couchi*; (F) *S. hammondi*.



TABLE 3.—The number of nonbreeding adult anurans recorded at varying distances from the breeding site (playa lake) and the habitat in which the species was recorded.

Distance (m)	Habitat	<i>Scaphiopus bombifrons</i>	<i>Scaphiopus couchi</i>	<i>Scaphiopus hammondi</i>	<i>Bufo cognatus</i>	<i>Bufo debilis</i>
0	dense grass	59	1	131	1	68
100– 300	sparse grass	66	34	72	16	7
300– 700	sparse grass	0	3	0	3	0
700–1100	grass-creosote	0	0	0	1	0
1200–1600	creosotebush	0	0	0	3	0

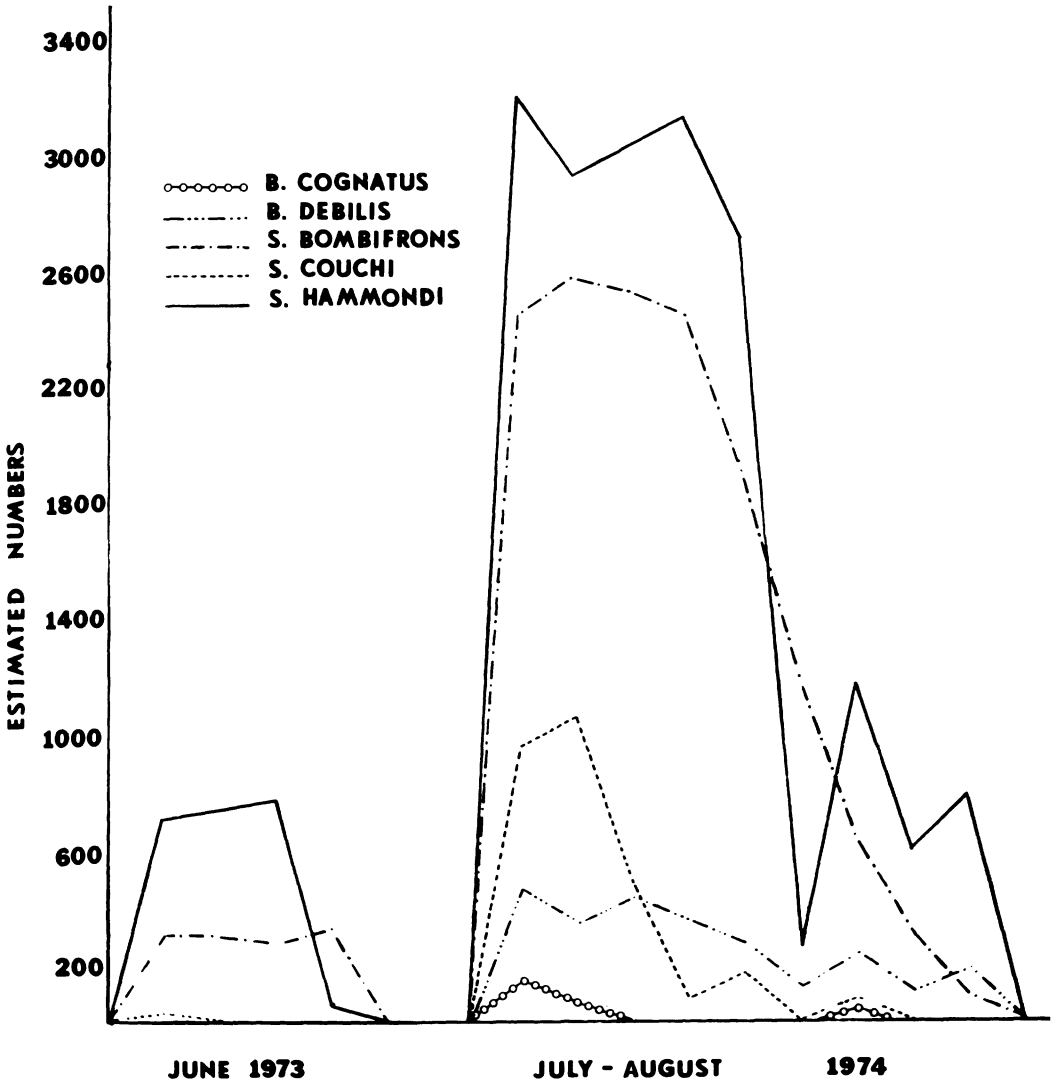


FIG. 8.—Estimated numbers of breeding adult anurans at the playa site. Data for June 1973, represent a year when only the cattle tank flooded; for July–August 1974, data were collected when the entire playa was flooded.



water playa habitats, with *S. bombifrons* males calling from scattered growths of the cocklebur, *Xanthium strumarium*. One species, *B. punctatus*, bred in rocky pools near the Doña Ana Mountains. *Bufo punctatus* remained at these pools for 3 days.

#### DISCUSSION

The juvenile stage is critical in the life cycle of desert anurans. The potential amount of fat and H<sub>2</sub>O storage undoubtedly varies as a function of size. Thus, juveniles must select habitats which maximize food availability and provide moist soil. Abundant food supply should result in rapid growth. Availability of moist soil reduces the probability of H<sub>2</sub>O loss and hence increases the number of days that these animals can forage.

Playa bottoms provide optimal habitat for juvenile anurans in the Chihuahuan desert because the soils are vertisols. These vertisols essentially prevent percolation and the dense grass cover (if not grazed) reduces evaporation, thus extending mesic conditions following even slight flooding. The surrounding fringe areas are aridisols in which sands fail to retain water for any appreciable length of time. This does not prohibit juveniles from utilizing the playa fringe areas, but 97.6% of all juveniles captured in our pitfall traps were taken on the playa bottom in flooding zones.

Another difference between the playa bottom and the surrounding fringe areas was duration of activity. Juveniles on the fringe areas were active only a day or two after a rain event, whereas juveniles on the playa bottom were active up to 55 consecutive days (Fig. 3). A toad should grow more rapidly in a habitat permitting many days of feeding activity than in one which greatly curtails feeding activity. Reduced feeding activity and increased aridity probably increases mortality of juvenile toads in the fringe areas.

Food is probably not limiting for juvenile toads on the playa bottom. Other studies indicate insect abundance is much greater

in the playa grasses than other habitats (Whitford, 1973, 1974). Crowding also does not appear to affect juveniles. As many as 73 juveniles have been captured at a single pitfall trap in a single day. During excavation on the playa bottom, incidental to this study, we found that most juveniles of all species followed the expansion fissures of the drying playa to the moisture, subsurface soils. Juvenile *S. bombifrons* and *S. hammondi* frequently would burrow 2-3 cm laterally from the fissure openings into the areas beneath the mud plates. Approximately 80% of the 831 juveniles excavated were unearthed within 15 cm of the surface during the day in the summer months. Many of the juveniles uncovered were touching individuals of their own and other species. The pressure to escape the heat and desiccation of the day apparently results in multispecies aggregates of juveniles in suitable microhabitats.

Juvenile *B. cognatus* ( $N = 26$ ) and *B. debilis* ( $N = 291$ ) were also excavated in these localities. However, many of the *B. debilis* juveniles followed large cracks in the surface and rodent burrows to depths  $> 15$  cm. Eleven adult *B. debilis* were also unearthed during another excavation project in the chambers of nests of the ant *Novomessor cockerelli*, in the arid fringe areas. Apparently no size classes of *B. debilis* dig their own burrows in contrast to the pelobatid species and *B. cognatus*, in which most individuals dig burrows.

Juveniles of all species aggregated in the relatively open, low depressions which are scattered over the playa. Most of these areas are  $< 2$ -m in diameter, but occasionally fill after a moderate rain and hold water for a day or two. These depressions are also the last areas to dry. The 15-m spacing of our pitfall traps gave us a representative sample of both the slightly elevated, more densely covered grass areas and the open depressions of the playa. Only 14% of our pitfall traps were located in depressions, but 62% of the 3102 juvenile

toads of all species were taken from depressions in the playa bottom. By aggregating on the wettest areas of the playa, juvenile toads were able to increase the number of days of activity on the playa.

The high mortality rate of juveniles can be accounted for by poor microhabitat selection and predation. As the playa dries, the soil of the more elevated areas hardens. Some toads are still active in the nearby depressions but feed in the elevated areas as well. The observations on mortality of juveniles seeking shelter under surface objects suggests that these animals may have died from heat. Temperatures at the soil surface under vegetative debris on the playa exceed 45°C. Dead toads removed from such debris were not shriveled (as is typical of desiccated toads) which suggests they died from something other than dehydration. We observed that juvenile toads are unable to dig into the hard playa soils, and thus must seek shelter in fissures or under surface debris. Fissures greater than 10 cm deep appear to provide the only microhabitat suitable for survival of young toads.

We observed predation by three species of snakes: *Heterodon nasicus*, *Masticophis flagellus*, and *Pituophis melanoleucus*. However, most mortality of juveniles probably occurs during the hibernation period from October through April, when juveniles must survive on fat stores accumulated during the summer.

The distribution of *B. punctatus* is best understood in its relationship to the other anurans in the area. *Bufo punctatus* reproduced in seven isolated rocky pools near the Doña Ana Mountains. Pelobatid tadpoles are carnivorous and grow more rapidly than *B. punctatus*, i.e., mean snout-vent length of 73 *B. punctatus* was 11.5 mm compared to 24.4 mm in 100 *S. bombifrons* and *S. hammondi* of the same age. The rocky pools used by *B. punctatus* for breeding are barren, offering little cover for tadpoles. The larger pelobatid tadpoles could eliminate all *B. punctatus* in unpro-

tested pools if tadpoles of both species co-occurred in the pools.

Cattle tanks on the bajada support breeding populations of the same species found in the playas at lower elevations. Water also accumulates in small rocky pools near the base of the mountains. Of the 11 pools located on or near our study area, 4 pools located within 100 m of a cattle tank had *S. couchi* and *S. hammondi*. Seven others more than 100 m from any cattle tank had only *B. punctatus*. No *B. punctatus* adults or tadpoles were found in any of the four pools in which pelobatids bred. The seven pools distant from any cattle tank supported a total population of 137 *B. punctatus* adults. There were no pelobatid tadpoles in any of these pools and all pools supported populations of *B. punctatus* tadpoles. The only discernible difference between pools was the presence or absence of the pelobatid species. This supports our contention that the pelobatid tadpoles cause the elimination of *B. punctatus* by eating the tadpoles.

One must use care when describing breeding sites of the "southwest." The breeding localities described by Bragg (1965) in northern New Mexico, Texas, Oklahoma and Arkansas are considerably more mesic than our site. Bragg reported few instances where more than two species occupied a given breeding site simultaneously. This is possible because Bragg's sites usually flood more than once during a season, permitting temporal segregation of habitat by species.

The probability of playas flooding on the Jornada Range is about one year in two or three. All species are forced to share breeding sites and times. Simultaneous calling of five species is typical in the natural playa breeding sites, although impoundments and roadside ditches may contain fewer species. With breeding sites and time at a premium, toads on the Jornada Range potentially face greater competition for suitable breeding habitat. This competition is avoided by differences in habitat preference and in mating calls.

Our data on habitat preference of breeding pelobatids support Bragg's (1965) observations that *B. cognatus* and *B. debilis* preferred grass clump habitats in the flooded playa. *S. hammondi* and *S. bombifrons* preferred open water areas. *S. couchi* bred in shallow areas with dense emergent grass.

It is well documented that anurans have evolved distinct calls (Blair, 1955; Littlejohn and Michaud, 1959; Bogert, 1960; Littlejohn, 1960; Martof, 1961; Michaud, 1962; Forester, 1973) and that females discriminate between calls of their own and related species. The potential for hybridization is greatest between toad species of similar size and ancestry. Bragg (1965) noted that *S. bombifrons* and *S. hammondi* are closely related. These species are also similar in size which increases the probability of a mistaken amplexus by the two species and hybridization as reported by Bragg (1965). Large *S. bombifrons* are close in size to small adult *S. couchi*, potentially permitting amplexus and possible hybridization between these species as well.

With a chorus of 6000–7000 males calling simultaneously from the same breeding site, each species must have distinctive calls to guide the females. The calls of each pelobatid species at our site are quite distinctive (Fig. 7). The calls of our *S. bombifrons* differ greatly from those of Forester's (1973) study. There are several plausible explanations for this difference: Forester may have recorded from hybrid populations, or our populations may exhibit character displacement as an adaptation to breeding in an area where temporal separation is not possible. Also it is possible that these species hybridize freely in the Chihuahuan Desert producing backcrosses with *S. bombifrons* with resulting hybrids resembling *S. bombifrons* morphologically.

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## RATE OF GASTRIC EVACUATION IN THE LIZARD, *ANOLIS CAROLINENSIS* (SAURIA: IGUANIDAE)

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**ABSTRACT:** Rate of gastric digestion (as measured by evacuation) by the iguanid lizard *Anolis carolinensis* of meals of crickets (*Gryllus* sp.) and mealworm larvae and adults (*Tenebrio molitor*), are compared at ambient temperatures of 32°, 25° and 18°C. The effect of large and small meal size, a 12-day starvation period and season are reported. Rate of evacuation was determined by comparing weight of dry matter consumed with dry matter remaining in the stomach at time of autopsy.

Little or no difference in percent gastric depletion at 32°C existed among the three food organisms at time intervals of 8, 16, 24 and 32 h of digestion. Approximately 25% of the meal was removed from the stomach after 8 h and 50% after 16 h. Thereafter, the rate of removal decreased slightly with the stomach reaching 90% depletion after 32 h. Gastric evacuation proceeded much more slowly at 25° and 18°C.

Statistical analysis revealed a significant rate difference for large and small meals and a 12-day starvation period, but no seasonal effect.

THE present work is a study of gastric digestion and evacuation in the lizard *Anolis carolinensis*. Amount of food moved through the stomach per unit time is a function of various environmental conditions and can be useful in estimating food consumption in nature. Lizards are well suited to provide data for comparing digestion rates because of ease of handling, maintenance, and the nature of the alimentary canal, although, as a group, they have received little attention (Englemann, 1966). The research that has been reported generally lacks quantification and no consistent methodology has yet emerged. Further justification for this kind of information comes from a growing interest in the derivation of working models for ecological systems and energy flow (Kitchell and Windell, 1972).

Riddle (1909) pioneered studies on the digestive powers or capacities of members of three groups of lower vertebrates in-

cluding one member of the Order Chelonia and determined the influence of season and temperature upon rate of evacuation. Lizard digestion was first studied (Knowlton, 1936) in *Uta s. stansburiana* and *Sceloporus g. graciosus* by force-feeding beet leafhoppers to determine the time required for their chemical breakdown beyond recognition. In a digestion study with the ringneck snake, *Diadophis punctatus arnyi*, Henderson (1970) determined the time interval between ingestion of food and the first defecation. An X-ray method has been used in digestion studies for following the course of digestion in the Florida indigo snake (*Drymarchon corais couperi*) and boa (*Constrictor constrictor*) (Blain and Campbell, 1942) and in the grass snake (*Natrix natrix*) (Skoczylas, 1970). A role for ambient temperature and behavioral-physiological correlates in feeding and digestion has been known for many years and is documented by numer-