Adaptations of the Amphibian, Scaphiopus couchi, to Desert Conditions[1]

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ABSTRACT: Spade-foot toads (*Scaphiopus couchi*) have been discovered recently in the Colorado Desert of California (Sonoran Desert), a region averaging approximately 2½ inches of rainfall per year and having very high summer temperatures (to 50 C). This is one of the driest and hottest areas in North America.

The species was apparently more widely distributed along the California side of the Colorado River in an earlier pluvial period. The animals now found there appear to be relict populations that have survived in a few isolated situations (in dry washes and at the edge of sand dunes), due to special environmental conditions.

Adults remain in burrows beneath dense vegetation during dry periods. Toads living at the sand dunes presumably bury themselves in a permanently wet layer in the sand. Adults appear to retain several layers of partially shed skin, which presumably form semi-impermeable membranes that reduce moisture loss. Body fluids of field animals just after emergence contain very high osmotic concentrations (approximately 20 o/oo compared to hydrated animals (7 to 8 o/oo). This also presumably tends to reduce water loss, perhaps even to aid in extracting moisture from a damp environment.

In the laboratory, eggs require less than 48 hours for hatching at room temperature, and tadpoles produce legs within ten days. Observations indicate they develop even more rapidly under field conditions. Young toads kept in the laboratory grew to approximately one-half adult size within three months.

An extreme local drought is currently in its 20th year. However, this drought has probably been exceeded in intensity in the not-too-distant past. Consequently, these conditions have probably been experienced by members of this species previously. Therefore, there is little reason to believe the present drought necessarily will eliminate the California populations of *S. couchi.*

INTRODUCTION

The distribution of Couch's spade-foot toad, *Scaphiopus couchi,* in the United States has been listed by Stebbins (1951) as southern Arizona, southern and eastern New Mexico, southwestern Oklahoma, and most of Texas except the extreme eastern part. Recently this species has been reported from California. Tinkham (1962) discovered these toads in a wash south of Needles, San Bernardino County, and Mayhew (1962) found them at Glamis, Imperial County. More important than the extended geographical range, however, is the ecological habitat in which these toads have been found. Although Bragg (1945) considers *S. couchi* one of the more xeric members of this terrestrial genus, the locality described previously by Mayhew (1962) appears to be entirely too hot and dry for any species of amphibian to survive successfully.

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U. S. Weather Bureau records (1954, 1958) for Brawley, Imperial County (the closest weather station) show that summer air temperatures reach 50 C at times, and remain above 43 C for many consecutive days. The mean annual rainfall is approximately 2½ inches. Occasional periods have occurred during which no measurable amount of rainfall was recorded for over a year. Turnage and Mallery (1941) found Brawley was the driest of 87 stations they investigated in the Sonoran Desert. This region is one of the driest in the United States, if not of all North America (Norris and Norris, 1961). Although rainfall records at Glamis are relatively few (see Mayhew, 1962), present information suggests Glamis receives even less precipitation than Brawley. For example, Brawley received a total rainfall of 6.01 inches during the past three years, whereas only 5.67 inches was recorded in my rain gauge at Glamis during the same period. Consequently, toads living in the Glamis area probably experience as little rainfall as any amphibians in North America.

The two California localities mentioned previously (Mayhew, 1962; Tinkham, 1962) are approximately 100 miles apart, suggesting that these toads were fairly widely distributed along the California side of the Colorado River in an earlier pluvial period. The animals that remain appear to be relict populations that have been able to survive in a few isolated situations in California's desert due to special environmental conditions that occur in these locations. It seems obvious these toads are using various mechanisms to survive in this region without being exposed to the harsh desert conditions that exist here. Consequently, this investigation was an attempt to identify some of these mechanisms.

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DISTRIBUTION

These toads emerge from their hiding places only following summer thunderstorms. *S. couchi* have been observed on the surface after rain storms in August and September, but have not been found following storms in October, December, or January. Since summer thunderstorms are very infrequent and widely scattered in southeastern California, one can find these animals only at irregular intervals at any given location. For example, a few toads were found east of the Algodones Dunes in September, 1961 (Mayhew, 1962). None were found in this location again until September, 1963, because no summer thundershowers occurred in this interval. However, during August,

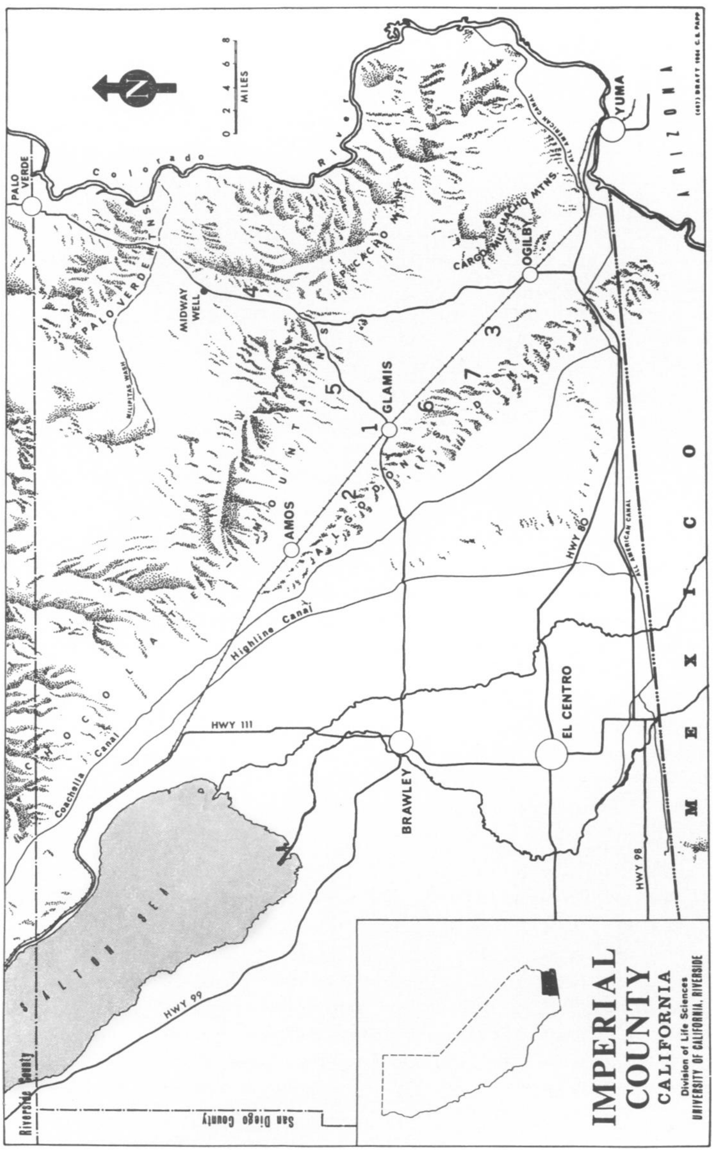

Fig. 1.—Map of Imperial County, California. Numbers refer to locations where *S. couchi* have been found. 1—Glamis; 2—near dunes 6 mi NW of Glamis; 3—Clyde; 4—Buzzard's Peak Wash; 5—Purgatory Wash; 6—edge of dunes 2 mi SE of Glamis; 7—beside dunes 7 mi SE of Glamis.

1963, these toads were found at an additional site. In the following September they were discovered in several localities in this portion of southeastern California, following the heaviest thunderstorm in over five years. These areas are indicated on Fig. 1. Although no toads were found at Glamis (Fig. 1, No. 1) in 1963, animals were discovered there in 1961 (Mayhew, 1962). Tadpoles were observed at a site on the edge of the Algodones Dunes six miles northwest of Glamis (Fig. 1, No. 2); railroad repairmen discovered an adult spade-foot toad at this point in a hole that they were digging beneath a railroad trestle. *S. couchi* were heard calling at a railroad siding named Clyde (Fig. 1, No. 3), 11 miles southeast of Glamis. Buzzard's Peak Wash, 16 miles northeast of Glamis (Fig. 1, No. 4) is the only site at which toads were found during both August and September, 1963. Tadpoles were found here in August, and adults in August and September. Purgatory Wash, (Fig. 1, No. 5) is six miles northeast of Glamis. Amplexing pairs were found in pools at the last two sites in September. Both tadpoles and young toads were discovered along the eastern edge of the Algodones Dunes, two miles southeast of Glamis (Fig. 1, No. 6; Fig. 2), but only tadpoles were seen near the dunes seven miles southeast of Glamis (Fig. 1, No. 7).

The presence of these toads along the eastern edge of the Algodones Dunes apparently is due to the runoff of rainfall from summer thundershowers along the western edge of the Chocolate Mountains, the Cargo Muchacho Mountains, and the Picacho Mountains (See Fig. 1). These areas receive scattered thundershowers during some summers, water from which flows toward the Algodones Dunes on its way to the Salton Sea. However, the dunes act as a large dam, and effectively stop water flow. Water then pools up along the eastern edge of the dunes (Fig. 2), and much of this water gradually sinks into the sand. The quantity of water occasionally impounded by the dunes is amazing. Glamis residents told me that about once every ten years or so they hunt ducks on lakes 10 feet deep along the eastern edge of these dunes.

Norris and Norris (1961) discussed the geology of these dunes in considerable detail. They suggested the luxuriant vegetation occurring at the ends of these washes probably is due to the temporary impounding of runoff water from infrequent rains. Thus, the moisture apparently is utilized by the vegetation, and in turn by the toads, that occur in this area (Fig. 3). Winter rainfall follows the same pattern of runoff. This moisture also probably benefits the toads at the edge of the dunes, even though the toads do not emerge in response to winter rains.

The exact distribution of these animals in the region shown in Fig. 1 still is unknown. Large pools of water occurred at Amos, northwest of Glamis (Fig. 1), on two occasions in 1963, but no toads appeared to call or lay eggs during the three weeks or so that water was present. A large pool three miles northwest of Amos produced the same result. Consequently, it is believed these toads have a dis-

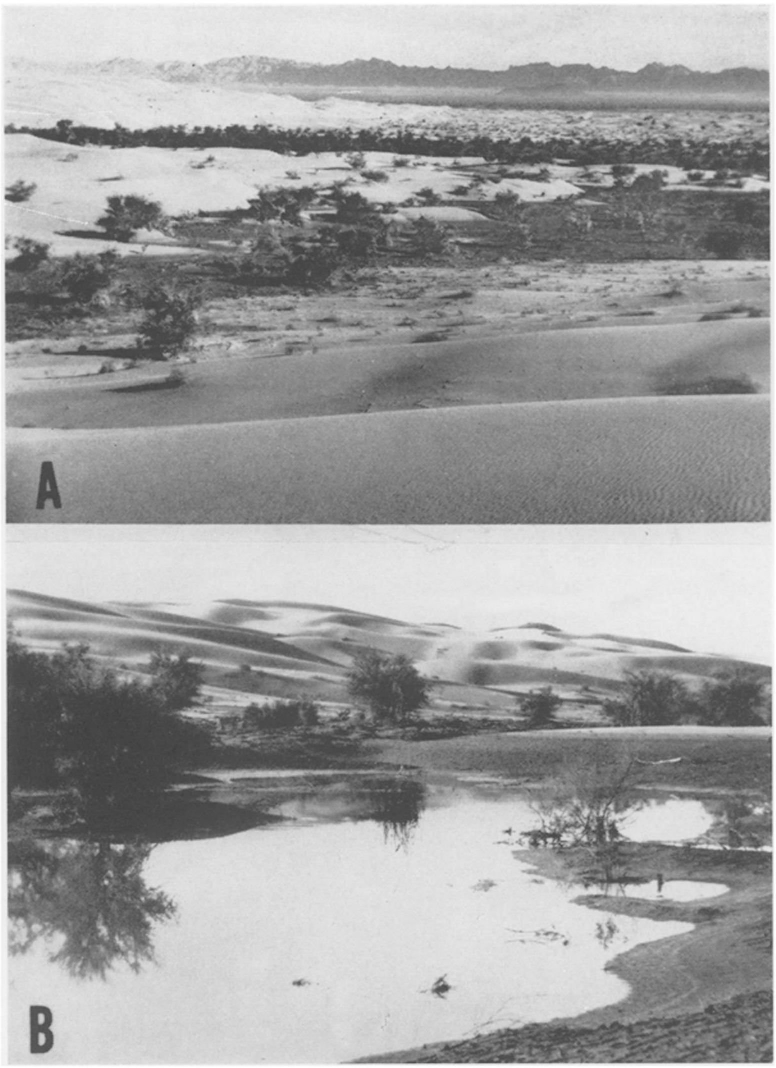

Fig. 2.—Runoff pool at eastern edge of Algodones Dunes one month after rain. A. Panorama of area surrounding pool (in dark area, left center). The entire dark area on both sides of the spur of sand in left center of photo had been under approximately 6 feet of water immediately following the storm, forming a pond between ¼ and ½ mile long. Chocolate Mountains in the background. B. Close view of pool. Palo verde (*Cercidium floridum*) in left center is approximately 12 ft high. Dispersing young *S. couchi* were captured near top of sand dune in center background, over ¼ mile from the pool.

Fig. 3.—Changes in vegetation as one approaches the eastern edge of Algodones Dunes near Glamis. A. Dunes as seen from Southern Pacific Railroad tracks. Dark line between bare area in foreground and dunes in background is composed of large creosote bushes (*Larrea divericata*), palo verde (*Cercidium floridum*), and ironwood (*Olneya tesota*). Creosote bush in left foreground is approximately one foot high. B. Closer view of dense vegetation near the dunes. Note top of dunes in right background. Creosote bush in right foreground is

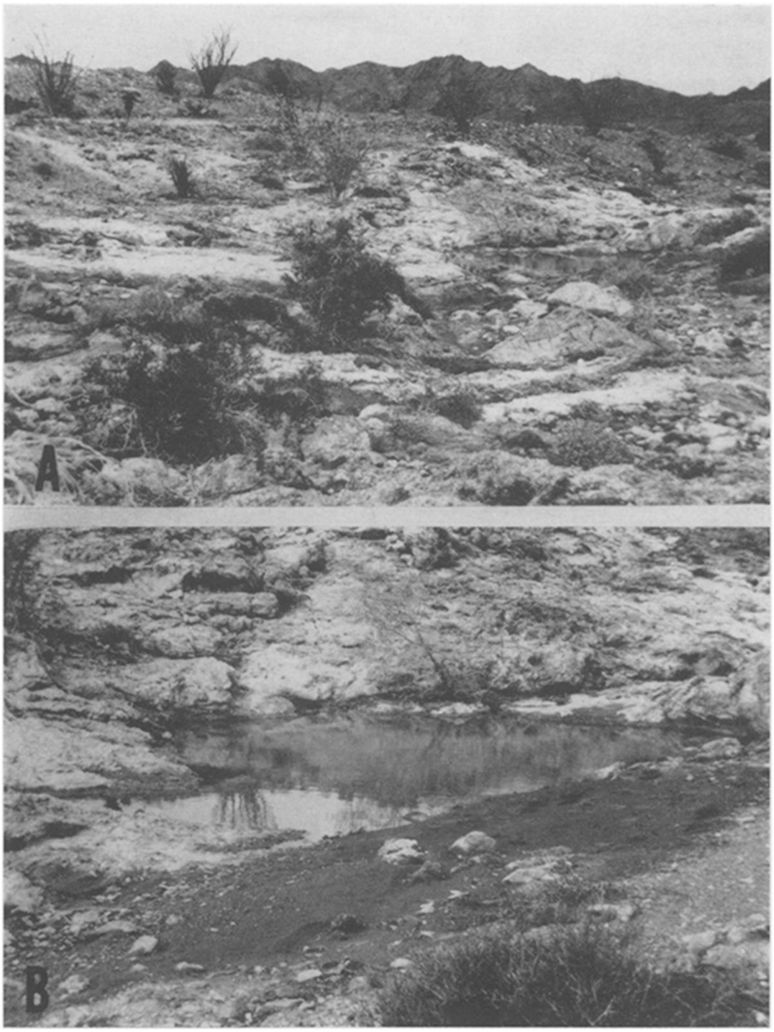

Fig. 4.—A "tank" at the edge of Purgatory Wash that holds water for long periods after a rain. A. Distant view of area surrounding pool, which is at right center. Creosote bush in left foreground is approximately 3 ft high. B. Close view of "tank" one month after last rain. At this time the pool was approximately 3 ft deep and 15 ft in diameter.

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approximately 3 ft high. C. Annual grasses, over 3 ft high, grow profusely between creosote bushes near the dunes. Many creosote bushes are 10 ft high. D. Ironwood and palo verde form dense thickets immediately adjacent to the dunes. Tallest palo verde at right center is approximately 18 ft high. Photo D taken by Lloyd Tevis.

tribution along the eastern side of the Algodones Dunes that terminates somewhere between Glamis and Amos.

The northern distribution of these toads in the dune area probably is controlled largely by the frequency with which runoff from summer thundershowers reaches the eastern edge of the dunes. The runoff which reaches the dunes in the vicinity of Glamis, south almost to Ogilby, comes from a much larger area than the runoff which reaches the dunes near Amos. Water is carried to the dunes in relatively few washes south of Glamis (see Norris and Norris, 1961, Fig. 1). Consequently, even though summer rains occur very infrequently at any one site, runoff from these storms should reach each wash terminus in the south-central portion of the dunes more often than corresponding locations in the northern part. Glamis residents have confirmed the fact that washes south of that hamlet carry water during the summer more often than washes north of Glamis.

S. couchi that are found along the Southern Pacific Railroad tracks near Glamis, contrary to what I thought earlier (Mayhew, 1962), apparently disperse from the dunes along the vegetated washes as far as sufficient shelter is available (approximately to the Southern Pacific tracks).

Buzzard's Peak Wash drains northward into Milpitas Wash, which in turn connects to the Colorado River (Fig. 1). Therefore, the toads found here probably represent a different population from the Algodones Dunes population. The fairly large number of *S. couchi* found in Buzzard's Peak Wash, and the numerous similar washes in the area, suggest a rather large toad population resides on the eastern side of the Chocolate Mountains. The major limiting factor in this region appears to be the number of breeding pools that can retain water sufficiently long to allow the toads to complete larval development. None of the pools discovered here thus far can retain water more than a week, even after a heavy storm. However, we found rocky natural "tanks" in Purgatory Wash (containing *Bufo punctatus* tadpoles, young and adult toads) that contained water more than one month following the September storm (Fig. 4). Presumably similar "tanks" occur in some of the washes east of the Chocolate Mountains, but we have been unsuccessful in locating them yet.

ADULT ADAPTATIONS

Several adaptations (behavioral, morphological and physiological) apparently are utilized by these animals to survive in this harsh desert region. A typical behavior pattern exhibited by *S. couchi* is the selection of burial sites beneath dense vegetation. Seventeen adult animals were released at Purgatory Wash one week following the September rain. These toads were released individually in the gravelly bottom of the wash, and each was observed until it disappeared beneath the soil. In 16 of 17 cases the animal moved under the nearest dense vegetation and buried itself (Fig. 5). These plants greatly reduce insolation reaching the soil beneath them. Therefore, soil temperatures are not as high here as in the open wash (example: 30.8 C at 50 cm beneath dense vegetation compared to 34.9 C at the same depth and time in open area 30 feet distant). This, in turn, reduces evaporation from the soil. Consequently, a toad buried in such a location probably would experience considerably less severe conditions than one buried at the same depth in the exposed wash.

Despite our efforts to uncover *S. couchi*, the depths to which these amphibians bury in this region still is unknown. However, the speed with which local *S. couchi* respond to rain or flowing water suggests they do not bury any great distance beneath the surface. Main *et al.* (1959) found species of *Helioporus* that live in sandy Australian habitats bury to depths of 26 to 33 inches, whereas *Neobatrachus* species that live in arid, compact soils are unable to bury themselves deeper than 12 inches. Perhaps *S. couchi* utilizes comparable depths.

Bagnold (1954b) stated it is well known that considerable moisture often is found close below the surfaces of sand dunes, even in very arid localities, and even though the spot may be far above the level of the desert floor. The reasons for this still are not entirely clear. He (Bagnold, 1954a) found a permanent moist layer in the sand 20 to 30 cm beneath the surface in the Sahara Desert, and Migahid and Abd el Rahman (1953) found a similar moist layer 50 to 75 cm beneath the sand surface in the Egyptian Desert. Holm (1960) reported a similar situation occurs in sand dunes in the Arabian Desert, al-

Fig. 5.—Burial site of adult *S. couchi* released in Purgatory Wash, marked by vertical stake in center foreground. Site is beneath an ironwood (*Olneya tesota*). Photograph by Lon McClanahan.

though he did not mention depth. Monthly soil samples were collected in the Algodones Dunes for three years (1959-1961). A corresponding permanently moist layer, 30 to 60 cm beneath the sand surface, also occurs in these dunes. Thus, it appears *S. couchi* that live near the dunes probably are able to dig sufficiently deep to reach a permanently moist layer in which they can spend the dry periods of the year.

These toads also appear to have a morphological structure that will aid in preventing excessive desiccation while buried. Animals were captured in September, 1963, in an area (Purgatory Wash) that had not received sufficient rainfall to produce a stream flow in over two years. Some animals were captured at this site just after they emerged. A few toads were partially covered with a black material that was dry and hard (Fig. 6). A closer examination of this material suggested it was composed of several layers of skin which had become loosened from the body, but not completely cast off. Later laboratory tests conducted on pieces of the material collected in the field indicated the substance probably is skin. It burns readily, producing the characteristic sulfurous odor of burning keratinous material. It is insoluble in dilute acid, alkali, and in a solution of the proteolytic enzyme pepsin (these are some of the usual tests for keratin [Hawk *et al.,* 1954]). Such a semi-impervious membrane presumably would considerably reduce the amount of evaporation from the animal's body. However, evaporation through the normal skin of these animals apparently is relatively slow for an amphibian. Chew and Dammann (1961) found *S. couchi* lost water through evaporation only about twice as fast as white mice, and four times as fast as the desert rodent, *Dipodomys merriami.*

A comparable covering has developed on captive *S. couchi* that were allowed to hibernate beneath sand for three months in the laboratory. The covering was not as thick as in the field toads.

Fig. 6.—Newly emerged *S. couchi* with much of the abdomen still covered with hard, black material. The wash in which this toad was captured had not contained surface water for at least two years prior to this time.

A body covering similar to this apparently can be produced experimentally in amphibians. The thyroid gland controls molt in these animals. Amphibians that experimentally lack a thyroid do not shed their skins completely, and the dead layers pile up until the animal appears much darker than normal (Goin and Goin, 1962). Perhaps reduced thyroid activity during the long hibernation of *S. couchi* produces this response in these toads.

McClanahan (1964) has conducted some physiological experiments on these Glamis toads. He found field animals just after emergence contained lymph and blood osmotic concentrations of 590 milliosmoles (approximately 20 o/oo) compared to a hydrated toad of 190 to 260 milliosmoles (7 to 8 o/oo). His recent evidence (personal communication) suggests most of this osmotic concentration is due to the presence of urea in the body fluids. His laboratory experiments on muscle contractility while exposed to various concentrations of different solutions have shown *S. couchi* muscles possess a rather high tolerance to hypertonic urea solutions. Muscle response is much greater in urea solutions than in the same concentrations of sodium chloride or sucrose solutions. This indicates muscle response is not merely dependent on osmotic concentration. Emerging toads (even after two years) did not appear to be severely dehydrated, and they were quite active. His experiments showed that urea concentrations within the range found in newly emerged toads do not hinder muscular activity to any great degree (70 to 100% of original activity). He feels this ability of *S. couchi* to tolerate hypertonic urea solutions is adaptive since these animals remain buried for many months of the year. In this state, they must produce urea from protein metabolism. This urea is presumably stored in body fluids while the toads are buried. Although McClanahan (1964) did not mention this possibility, it seems obvious such a high osmotic concentration would tend to slow down water loss to the surrounding soil. It might even allow the toads to acquire some moisture from their surroundings, if the animals were buried in damp sand. Thus, the stored urea could provide additional benefits.

ADAPTATIONS OF EGGS AND YOUNG

Tadpoles of *S. couchi* were found in Buzzard's Peak Wash following the August, 1963, storm. However, the pools in this wash did not survive long enough for tadpoles to mature, and tremendous mortality occurred. Despite the heavy September rain, we were unable to find any pools in Buzzard's Peak Wash that we were sure would survive long enough to produce young *S. couchi* this year. At the edge of the Algodones Dunes, however, large pools developed in which tadpoles were found in September, and young toads were discovered nearby in October (Fig. 2). Some young toads were found dispersing over the dunes from the pools; they were over ¼ mile from the nearest pool, and over 100 feet above the water. Consequently, a successful hatch occurred in the pools near the Algodones Dunes during 1963.

The amplexing pairs of *S. couchi* captured in Buzzard's Peak Wash and at Purgatory Wash eventually laid eggs in captivity. Observations on tadpoles produced from eggs hatched in the laboratory and in the field suggest that young *S. couchi* possess several adaptations to help them survive in this inhospitable environment. For example, egg development is extremely rapid in this species, as in other *Scaphiopus* (Bragg, 1945). Tadpoles hatched in the laboratory within 48 hours of the time eggs were laid (eggs maintained at room temperature). These tadpoles were feeding on rolled oats within 72 hours. However, the developmental rate in the laboratory was slower than that occurring in nature, since field tadpoles collected one week following the rain were twice the length and twice the volume of laboratory tadpoles produced during the same storm. Consequently, field eggs probably developed more rapidly than eggs in the laboratory.

Some tadpoles grow much faster than others. Two size groups of *S. couchi* tadpoles were found in the pools at Buzzard's Peak Wash in August. The large tadpoles were separated from the smaller ones, and the water was changed on the small ones. Following this, some small tadpoles suddenly (within 24 hours) became large ones. Each time such a separation was performed, additional large tadpoles developed. In one case, an extremely small animal was separated from all the others and placed in its own bowl. Within a few days it had increased in size to that of the other small tadpoles. The implication is that some sort of inhibitor is produced by the early-developing tadpoles to restrict the growth of the additional ones. This situation is not unique, since Richards (1958, 1962), Rose (1960) and West (1960) have found growth inhibitors that restrict tadpole development in other amphibian species.

Tadpole development in *S. couchi* is also exceedingly rapid. Young tadpoles in the laboratory had four legs within ten days following the rain in which the eggs were produced. Sizable young toads have been found in the field within four weeks of the time of egg laying. Presumably they metamorphosed a number of days preceding their discovery.

Once metamorphosis has occurred, young spade-foot toads grow at a rapid rate. In a three-month period in the laboratory (at room temperature), three toads have averaged 110% increase in length and over 1,100% increase in weight (Fig. 7). Based on the average measurements of 14 adult *S. couchi,* the largest of these young toads now is about one-half as long (47 vs. 80 mm) and about one-half as heavy (15 vs. 31 gm) as the adults. Presumably growth would have been more rapid in the field than in the laboratory, judging from tadpole growth data. These animals are capable of growing very rapidly in the interval between metamorphosis and hibernation for the first winter.

Bragg (1945) found most *Scaphiopus* tadpoles (except *S. couchi*) cannibalistic. However, *S. couchi* tadpoles apparently are cannibalistic at times. Several newly metamorphosed animals were observed being devoured by tadpoles in the laboratory. The metamorphosed toads appeared to be in a somewhat weakened condition immediately prior to being attacked. However, I never observed tadpoles eating other tadpoles, no matter what their physical conditions.

DISCUSSION

S. couchi that live in the Glamis area survive under gross environmental conditions that are considerably more rigorous than members of this species experience in other parts of the range. However, to date all known characteristics of the Glamis population also are present in other populations. For example, the very high osmotic concentrations (up to 20 o/oo) found in newly emerged Glamis toads also appear in newly emerged Arizona toads (McClanahan, 1964; pers. comm.). Glamis toads are unable to reproduce every year because of weather conditions. However, Bragg (1945) has stated that in Oklahoma "in any given area spade-foots may not breed at all during a year (or several years) if conditions fail to be suitable." Therefore, all *S. couchi* probably possess the necessary characteristics to survive under difficult conditions, but the California populations are living at the maximum levels of tolerance for the species. The breeding season of Glamis *S. couchi* is not adapted to optimal local conditions, since most rainfall occurs in the winter here, and these toads do not respond to winter rains (see Mayhew, 1962). Rather, the breeding cycle is attuned to the summer rainfall areas where the vast majority of this species resides.

These toads are experiencing a period of extreme drought at the present time (now entering the 20th year). The United States De-

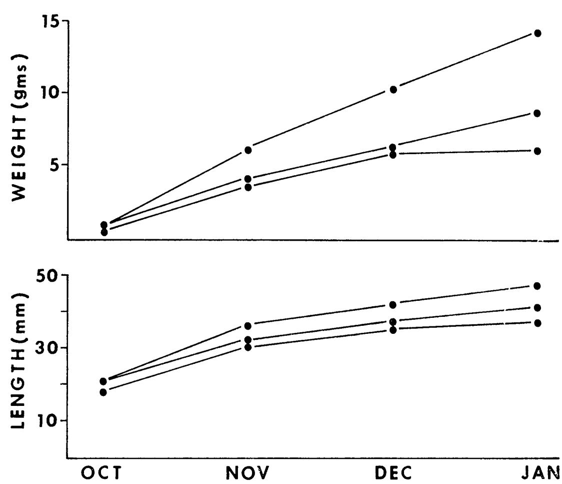

Fig. 7.—Growth rates of three young *S. couchi* captured at the Algodones Dunes one month after they hatched and maintained at room temperature in the laboratory for the following three months.

partment of Interior (1951) indicated this was one of the eight most severe droughts in the southwestern United States since the 13th century. From his tree-ring research, Schulman (1945) stated the 27-year period from 1571 to 1597 was the driest in the Colorado River Basin since 1300. He has also shown (Schulman, 1947) a close correlation between the Colorado River Basin and Southern California droughts. He later reported (Schulman, 1956) that the 85-year period from 1215 to 1299 was the driest on record for this region. In 1956 he considered the present drought to be the driest since the 1200's.

The general conclusion is that the current drought is a very severe one, but has been exceeded in the not-too-distant past. Consequently, this amphibian species apparently has been exposed to conditions equally severe before. It appears man's activities that lower water tables, etc., are more likely to cause the demise of these toad populations than the present drought *per se.*

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