Cross Reference: Turner; Medica; reptiles; lizards; flat-tailed horned lizard; Phrynosoma; distribution; abundance

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The Distribution and Abundance of the Flat-tailed Horned Lizard (*Phrynosoma mcallii*)

FREDERICK B. TURNER AND PHILIP A. MEDICA

The occurrence of the flat-tailed horned lizard (*Phrynosoma mcallii*) was investigated in 458 sections (each 2.59 km²) in Riverside, San Diego and Imperial counties, California, in 1979. In all sections, 40 *P. mcallii* (0.09/man-hour) and 2,191 horned lizard scats (4.8/man-hour) were counted. When sections were grouped in 12 general areas, mean numbers of horned lizards ranged from 0.40/hr (north of Benson Dry Lake) to 0.00/hr (northern East Mesa, Coyote Wells area). The density of *P. mcallii* in a plot in the Yuha Basin (40 km west of El Centro) was 6–8/ha. The flat-tailed horned lizard is similar to *P. platyrhinos* in terms of sex ratio (1:1), age at maturity (20 months), and ability to lay more than one clutch of eggs in favorable years. Mean home ranges for five male and four female *P. mcallii* (estimated as convex polygons) were 0.13 ha and 0.05 ha, respectively. *P. mcallii* feeds almost exclusively (>95% of items) on ants. The most commonly consumed species are harvester ants (*Veromessor pergandei*, *Pogonomyrmex californicus* and *P. magnacanthus*). In 1980 the relative abundance of *P. mcallii* (L), density (P), diversity (Δ_1) of perennial plants and relative abundance of harvester ants (A) were estimated in ten plots in southeastern California. The abundance of the lizard was positively correlated ($r = 0.93$) with perennial density, and a clear positive association between lizard and ant densities was exhibited in nine of the ten plots. A regression model accounted for 91% of observed variation in lizard density, and predicted relative abundance of *P. mcallii* as:

$$L = 75.0P + 8.6\Delta_1 - 0.04A - 7.9$$

At present, *P. mcallii* is not an endangered species. However, the original geographic range of this lizard has been diminished, and the species is not as abundant in certain parts of its range as it once was. Such changes have probably been brought about by human activities. *P. mcallii*, like many other desert species, is not in immediate danger of extinction but stands in jeopardy because of continued alteration or destruction of its habitat.

THE flat-tailed horned lizard (*Phrynosoma mcallii*) occurs in desert areas of southeastern California, southwestern Arizona and adjoining portions of Sonora and Baja California Norte, Mexico. The species often exists at apparently low densities in areas where it occurs. With regard to the relative abundance of lizards in San Diego County, Klauber (1939) commented: "Probably the rarest . . . [is] . . . *Phrynosoma m'callii* on the desert." Norris (1949) observed that near Palm Springs the capture of *Phrynosoma mcallii* "was not a common occurrence," and that, "If two specimens were taken in a day . . . collecting was good." However, between February 1961 and October 1964, 502 *P. mcallii* were collected (or found dead) along an 11.2 km stretch of Highway 78 between the Coachella and East Highline Canals (Wilbur Mayhew, pers. comm.). In May 1963 Mayhew concluded that *P. mcallii* was the most abundant reptile occurring in the creosotebush scrub between these canals. In 1964, these horned lizards were not as abundant as in previous years, and by the early 1970's numbers of *P. mcallii* along this once well-populated roadway were further reduced.

Because of these observations and because of increasing use and development of desert areas in Riverside and Imperial counties, concern as to the status of *P. mcallii* was expressed by Stewart (1971) and (in 1973) by staff of the Museum of Vertebrate Zoology in Berkeley. Similar views were expressed through the Planning Commission of Riverside County. The Office of Endangered Species of the US Fish and Wildlife Service responded by designating *P. mcallii* a species whose status should be reviewed. Assessment of the distribution and abundance of this lizard, clarification of important characteristics of its habitats, and development of sound conservation policies are important needs, because this species often coexists with sources of natural gas, oil, geothermal energy and minerals, or occurs in areas of value for agricultural or recreational uses.

Between 1978 and 1980 the Bureau of Land Management supported investigations of the status of *P. mcallii* in California. The purpose of this work was to determine the local distribution and relative abundance of *P. mcallii,* to correlate these parameters with various habitat attributes, and to gather information on the structure of the populations and mobility and food habits of individual lizards.

METHODS

In 1978 the density of *P. mcallii* was estimated in a 210 × 210 m (4.1 ha) plot in the Yuha Basin, about 40 km west of El Centro, California (designated Plot 15 during the 1978 work). Capture-recapture data were analyzed as a chain of samples (Schumacher and Eschmeyer, 1943). Home range estimates were derived for lizards captured three or more times in this plot. Capture loci were mapped and outermost points connected to form convex polygons.

In 1979 field work was carried out between 19 April and 29 July over much of the geographic range of *P. mcallii* in California. The basic element of the work was the "section search"—a one-hour walk through the 2.59 km^2 in question. Field workers maintained records of *P. mcallii* observed (including dead ones), numbers of horned lizard scats counted, numbers of other species of lizards observed and numbers of nests of black (*Veromessor pergandei*) and red (*Pogonomyrmex californicus, P. magnacanthus*) harvester ants counted.

Scats of *P. mcallii* were collected from various areas in both 1978 and 1979. Ants and ant remains in scats collected in 1978 were identified by Roy Snelling of the Los Angeles County Museum of Natural History. Identifications of ants in scats collected in 1979 were made by Robert M. Chew.

In 1980 ten study sites (5 pairs) were established in various parts of Imperial and eastern San Diego counties, California. Locations of these sites are available on request. One member of each pair was good habitat and one apparently poor habitat (based on assessments made in 1979). In each of these areas we estimated the relative abundance of *P. mcallii,* the abundance and diversity of perennial plants, and the relative abundances of harvester ants. Two people worked from 3–5 days in each of ten plots. Each plot was inspected by both workers for 1.5 hr each morning, and numbers of *P. mcallii* and horned lizard scats tallied. Counts of lizards and scats were converted to counts per man-hour and an index of lizard abundance (L) computed as 15 (lizards/man-hour) + 5 (scats/man-hour). All perennials occupying fifty 50 × 2 m belt transects in each plot were tallied by species. Diversities of perennial plants were computed as Δ_1 (Hurlbert, 1971):

$$\Delta_1 = [N/(N - 1)]\left(1 - \sum_{i=1}^{S} p_i^2\right) \quad (1)$$

where N = the total number of individuals in the census, S = the number of species in the census, $p_i = N_i/N$, and N_i = the number of individuals in the i_{th} species in the census.

All active nests of *Pogonomyrmex* spp. and *Veromessor pergandei* were counted in study areas. Numbers of foraging workers in selected nests were estimated. We used a mark-recapture procedure described by Porter and Jorgensen (1980), in which large numbers of ants were collected and marked with fluorescent dyes. Numbers of workers (N) in a nest were estimated from the number of ants marked in the first sample (a) and the number of ants recaptured (r) in the second sample (n), as recommended by Bailey (1952):

$$N = a(n + 1)/(r + 1) \quad (2)$$

Mean numbers of workers per nest were calculated from nest sampling data for each plot. An index of harvester ant abundance (A) was computed for each plot by i) multiplying the number of active nests of *Veromessor pergandei* (V_n) by the mean number of workers per nest (V_d), ii) multiplying the number of active nests of *Pogonomyrmex* spp. (P_n) by the mean number of workers per nest (P_d), iii) summing these products and multiplying by 10^{-4}:

$$A = 10^{-4}(V_n V_d + P_n P_d) \quad (3)$$

Further information on the relationship between the relative abundance of *P. mcallii* and harvester ants was collected in areas 11–23 km east of Yuma, Arizona, during early June 1980.

RESULTS

Distribution and abundance of Phrynosoma mcallii.—Counts were made of *P. mcallii* and horned lizard scats in 458 sections in southeastern Cal-

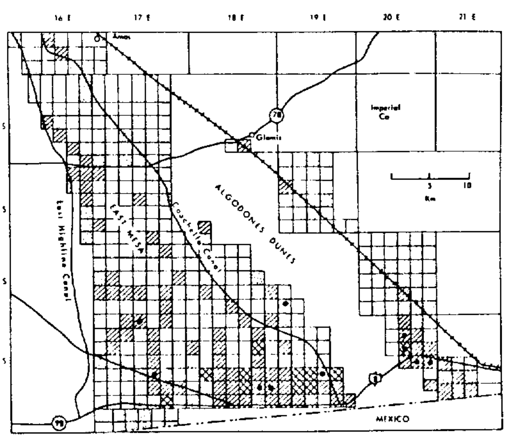

Fig. 1. Results of section searches in southeastern Imperial County, California. Observations of *Phrynosoma mcallii* are indicated by black dots. Light stippling: no horned lizard scats; diagonal lines: 1–14 horned lizard scats; cross-hatched: 15 + scats.

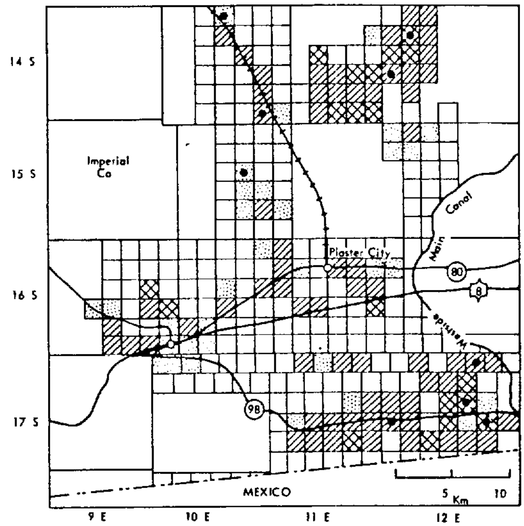

Fig. 3. Results of section searches in southwestern Imperial County, California. Section codes as in Fig. 1.

ifornia during 1979. Figs. 1–3 illustrate some of the sections examined and results of observations. Similar maps illustrating work in northern Imperial and Riverside counties are available on request.

For ease of analysis, sections were grouped in 12 general areas on grounds of geographic contiguousness and similarity of habitats (Table 1). Table 2 gives observations of horned lizards and counts of scats according to time of season. A "mean time of season" for each area was calculated by assigning a value of 1 to the period 15–28 April, a value of 2 to 29 April–12 May, etc., and computing weighted means. A "mean time of day" was computed by assigning a value of 6 to the time interval 0500–0659, a value of 8 to the time interval 0700–0859, etc., and computing weighted means. Mean numbers of *P. mcallii* counted per man-hour were taken as dependent variables, and mean time of season and mean time of day for each area were taken as independent variables. Multiple regression analysis showed that the multiple *R* associated with time of day was 0.447 ($R^2 = 0.20$), and with both independent variables was 0.450 ($R^2 = 0.20$). While Table 2 shows that season influenced success in counting *P. mcallii* and scats, the regression analysis shows that season was not a significant factor in the geographic variation expressed in Table 1.

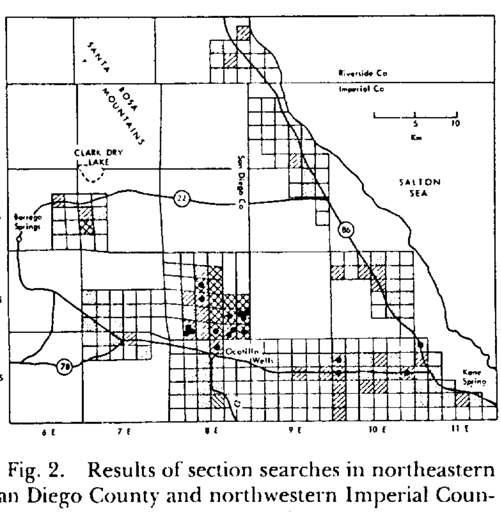

Fig. 2. Results of section searches in northeastern San Diego County and northwestern Imperial County, California. Section codes as in Fig. 1.

Counts of horned lizards and scats in sections were used to compute indexes of the relative abundance of *P. mcallii* in 65 townships. Indexes were computed by scoring one point for each scat counted, 50 points for each lizard observed, and dividing the total points for a township by the number of sections examined. Abundance indexes ranged from zero to 58, but few indexes exceeded 15. Results of this procedure are illustrated in Fig. 4. This map shows at least four areas where the flat-tailed horned lizard is well represented today: the southern part of East Mesa (T15–16S, R17–

TABLE 1. OBSERVATIONS OF HORNED LIZARDS (*Phrynosoma mcallii*) AND COUNTS OF HORNED LIZARD SCATS IN 12 AREAS IN SOUTHEASTERN CALIFORNIA DURING 1979.

General area	Lizards observed	Scats counted	Lizards per hour	Scats per hour
1 Ogilby	4	90	0.13	2.9
2 southern East Mesa	6	515	0.06	5.2
3 northern East Mesa	0	54	0.00	1.4
4 Durmid	2	84	0.05	2.0
5 Riverside County	1	96	0.02	2.3
6 Borrego Sink, Clark Lake	0	23	0.00	3.1
7 Kane Spring	4	109	0.09	2.5
8 Borrego Mountain	14	463	0.40	13.2
9 Superstition Mountain	4	249	0.11	6.9
10 Plaster City	1	49	0.04	2.0
11 Coyote Wells	0	65	0.00	3.8
12 Yuha Basin	4	394	0.10	9.4

20E), and particularly south of Ogilby in the vicinity of Gray's Well (T16S, R19–20E); the southeastern portion of the Yuha Basin and the vicinity of Signal Mountain (T16–17S, R12E); south of Superstition Mountain (T14S, R10–11E) and north of Ocotillo Wells and Benson Dry Lake (T11S, R8E). Fig. 4 fails to indicate one other favorable area—the vicinity of Borrego Springs. Few sections were examined in this area, but there are numerous reports of *P. mcallii* just east and northeast of Borrego Springs and near Clark Dry Lake (Glenn Stewart and Tom Sinclair, pers. comm.).

Abundance indexes were regressed on numbers of sections examined. This analysis showed a highly significant non-zero slope ($F = 28.3$, $F_{0.01} = 7.0$), indicating that abundance indexes were dependent on effort (i.e., higher abundance indexes tended to be associated with larger numbers of sections examined per township). Hence, the distribution of *P. mcallii* within a township (93.2 km²) is not homogeneous, and as more extensive searches are made the probability of discovering a favorable site is enhanced. It follows, then, that township abundance indexes based on searches of only a few sections are questionable. We also considered the effect of different weightings of lizards and scats on abundance indexes. Abundance indexes were computed for townships with lizards weighted 20:1, 10:1, 5:1 and 1:1 relative to scats. The four most highly ranked townships retained their order regardless of weighting, and the order of the top seven was only slightly changed by different weightings.

Natural history of Phrynosoma mcallii.—Of 52 adult horned lizards registered in 1978, 30 were males and 22 females. Mayhew's field notes referred to sex ratios of samples collected near

TABLE 2. OBSERVATIONS OF HORNED LIZARDS (*Phrynosoma mcallii*) AND COUNTS OF HORNED LIZARD SCATS DURING 1979.

Dates	Man-hours	Lizards observed	Scats counted	Lizards per hour	Scats per hour
Apr. 15–28	58	8	305	0.14	5.3
Apr 29–May 12	181	15	755	0.08	4.2
May 13–26	79	12	588	0.15	7.4
May 27–Jun 9	61	3	304	0.05	5.0
June 10–23	45	2	108	0.04	2.4
June 24–	34	0	131	0.00	3.9

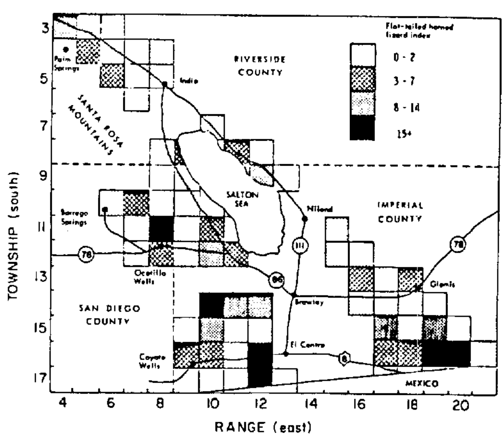

Fig. 4. Relative abundance of *Phrynosoma mcallii* in 65 townships in southeastern California.

TABLE 3. ANALYSIS OF MAY CAPTURE-RECAPTURE DATA FOR *Phrynosoma mcallii* IN PLOT 15. X_t is the number of marked individuals at risk just before the t_{th} sample, n_t the number of individuals in the t_{th} sample, and x_t the number of marked individuals in the t_{th} sample.

Dates	X_t	n_t	x_t	x_tX_t	$n_tX_t^2$
May 9	6	9	1	6	324
May 10–15	14	11	6	84	2,156
May 16	19	24	17	323	8,664
Totals				413	11,144

TABLE 4. ESTIMATED HOME RANGES OF NINE HORNED LIZARDS (*Phrynosoma mcallii*) IN IMPERIAL COUNTY, CALIFORNIA.

Number	Sex	Number of captures	Size of convex polygon (m^2)
11	m	6	2,112
12	f	3	45
13	m	3	804
18	m	4	934
19	f	4	487
21	f	4	1,288
24	m	7	824
25	m	4	1,763
27	f	3	214

Glamis and of lizards used in a laboratory experiment. Of 65 lizards, 29 were males and 36 females. Neither our findings nor Mayhew's represent significant departures from an expected sex ratio of 1:1. Assuming yearling males to range from 9–11 g and yearling females from 8–12 g (among May lizards in Plot 15), the mean weight of five young males was 9.8 g, that of six young females 9.3 g. Mean weights of 22 other males and 15 other females were 16.0 and 17.8 g, respectively. Female *P. mcallii* are probably not sexually mature until an age of around 20 months. *P. mcallii* may lay more than one clutch of eggs in favorable years, and two clutches were laid by most females in 1978. Young from the first clutch hatched during July. Three hatchlings were captured on 7 Aug., 1978, and were 35–36 mm snout–vent weighing 1.5 g each. Young from the second clutch probably hatched during late Aug. or early Sept. Hatchling lizards captured 21 Sept. 1978, measured 34 mm s–v length (second clutch) and 40 mm s–v (first clutch), and weighed 2 and 3 g, respectively. In terms of population structure, age at maturity, and reproductive potential, *P. mcallii* is similar to *P. platyrhinos* in southern Nevada (Medica et al., 1973).

Capture-recapture data for *P. mcallii* in Plot 15 during May 1978 were arranged for analysis as indicated in Table 3. The population estimate is 11,144/413, or ~27. Given a study area of 4.41 ha, the estimated density of *P. mcallii* in Plot 15 was around 6.1/ha. On the evening of 26 June and the morning of 27 June, Plot 15 was reexamined in order to see if horned lizards were still active at this time of the year. On 26 June two new and four previously marked lizards were taken. If these data are combined with the earlier capture-recapture data (from May) the number of lizards in Plot 15 would be estimated as around 34.2, with a corresponding density of 7.8/ha.

Loci for horned lizards captured three or more times in Plot 15 were used to compute sizes of home ranges (convex polygons). Table 4 gives estimated home ranges of nine horned lizards. All of these estimates suffer from an unknown amount of sample size bias. We have not made bias corrections (Jennrich and Turner, 1969) because we have no idea of the nature of the utilization distribution exhibited by *P. mcallii* (Turner, 1971). Although we must assume that the polygon areas are underestimates of true home ranges, it is worth noting the contrast in areas of male and female polygons. The mean of the five male home ranges was about 1,287 m^2 and all exceeded 800 m^2 in extent. The mean of the four female home ranges was about 509 m^2, and only one exceeded 500 m^2. Turner et al. (1969) analyzed home ranges (*HR*) of terrestrial lizards and derived the following relationship between home range size (m^2) and body weight (*W*, g):

$$HR = 171.4W^{0.95} \quad (4)$$

All species reviewed by these authors with body weights from 15–20 g had estimated home ranges of less than 1 ha. Equation 4 predicts a home range of around 0.25 ha for *P. mcallii* (based on a body weight of 17 g).

P. mcallii apparently feeds almost exclusively on ants, to a significantly greater degree than many other species of the genus (Pianka and Parker, 1975: Table 6). Based on an examination of 106 stomachs Pianka and Parker reported that 97.2% of the prey items were ants. Snelling's counts of 4,316 items in 16 scats of *P. mcallii* collected in 1978 showed 97.7% to be

TABLE 5. DATA PERTAINING TO HORNED LIZARDS, PERENNIAL PLANTS AND HARVESTER ANTS IN TEN PLOTS IN SOUTHEASTERN CALIFORNIA.

Plots	Number of *Phrynosoma mcallii* counted	Number of horned lizard scats counted	Horned lizard abundance index	Aggregate density of perennial plants (n/ha)	Diversity of perennials	Number of active nests of *Veromessor pergandei*	Number of active nests of *Pogonomyrmex* spp.	Mean number of workers (×10³) per nest (*Veromessor*)	Mean number of workers (×10³) per nest (*Pogonomyrmex* spp.)	Ant abundance index
1	0	14	10.0	2,326	0.705	27	0	16.5	—	44.6
2	0	12	5.0	810	0.706	25	2	7.9	—	19.9
3	1	29	13.3	2,480	0.213	19	0	12.0	—	22.8
4	3	23	17.8	2,796	0.659	65	3	12.2	—	79.5
5	0	1	0.4	1,020	0.460	47	0	12.4	—	58.3
6	1	21	13.3	2,064	0.620	9	2	5.7	—	5.2
7	0	6	2.5	724	0.446	0	4	—	—	0.2
8	0	2	0.8	1,172	0.332	9	2	6.7	—	6.1
9	0	0	0	268	0.604	0	7	—	0.5	0.4
10	0	6	2.5	1,094	0.326	11	1	16.5	0.7	18.2

remains of ants. Numbers of ants in scats ranged from 27 to 1,229. Although remains of at least 11 species were observed, four species—*Veromessor pergandei* (24%), *Pogonomyrmex californicus* (22%), *P. magnacanthus* (29%) and *Conomyrma insana* (16%)—made up almost 92% of all counted.

Over 6,900 ant heads in 74 samples collected from various sections in 1979 (285 scats) were identified by Robert Chew. *Veromessor pergandei* and *Pogonomyrmex* spp. occurred in about 88% of the samples and *Conomyrma* spp. (mostly *C. insana*) and *Myrmecocystus* spp. in 74% of samples. Only five kinds of ants were common (≥10%) in scats: *Veromessor pergandei* (36%), *Pogonomyrmex californicus* (23%), *P. magnacanthus* (10%), *Conomyrma* spp. (14%) and *Myrmecocystus* spp. (13%). Harvester ants and *Conomyrma* spp. accounted for 83% of all ants in scats (cf. 92% in the more limited 1978 samples).

Environmental factors and relative abundance of P. mcallii.—Observations in 1979 generally failed to show correlations between the abundance of *P. mcallii* (as indicated by counts of lizards and/or scats) and i) counts of harvester ant nests, and ii) counts of other lizards. The one statistically significant correlation was between counts of horned lizards and counts of nests of *Veromessor pergandei*. Although statistical correlations were insignificant, *P. mcallii*, *Callisaurus draconoides* and *Dipsosaurus dorsalis* were often observed together.

The 1980 field work incorporated an important improvement, viz., an attempt to estimate harvester ant colony sizes rather than simply count nests. Plot-specific summaries of sampling data from the ten 1980 plots are given in Table 5. Only five *P. mcallii* were observed in the course of 106 man-hours of search, about half the rate experienced in 1979. One-hundred-and-fourteen scats were counted (1.08/man-hour), again distinctly less than the rate in 1979 (4.8/man-hour). Predominating shrubs in every plot were *Larrea tridentata* and *Ambrosia dumosa*. Numbers of perennial species counted in plots were usually from 5–7, so species richness was modest. Far more nests of *Veromessor pergandei* were counted (212) than of *Pogonomyrmex* spp. (21). Numbers of foragers were estimated for 57 nests of *Veromessor* and three nests of *Pogonomyrmex*. Estimated numbers of foraging *Veromessor* per nest ranged from 737 to ~38,000, and plot means ranged from around 6,000 (Plot 6) to 16,500 (Plots 1, 10).

The relative abundance of *P. mcallii* inferred from 1979 data and the 1980 abundance indexes were in good accord, although contrasts between Plots 7 and 8 and 9 and 10 (in 1980) were not as pronounced as those observed in 1979. A rank correlation test of the indexes from 1979 and 1980 (Snedecor, 1956:190) gave r_s + 0.8, which is significant at the 1% level.

The abundance of *P. mcallii* was examined by stepwise multiple regression analysis of the 1980 data, using aggregate perennial density (P), perennial diversity (Δ_1), and harvester ant abundance indexes (A) as independent variables. The

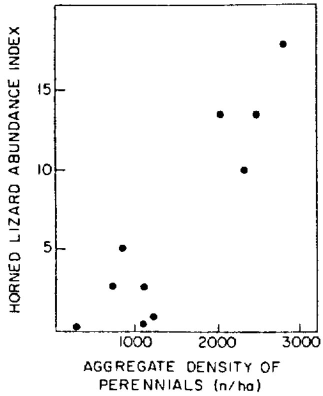

Fig. 5. Relative abundance of *Phrynosoma mcallii* and total density of perennial plants in ten areas in southeastern California.

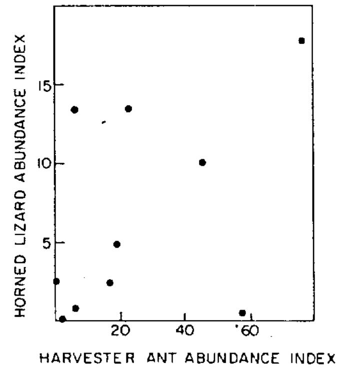

Fig. 6. Relative abundances of *Phrynosoma mcallii* and harvester ants in ten areas in southeastern California.

regression model explained about 91% of the observed variation in the dependent variable, and predicts horned lizard abundance as:

$$L = 75.0P + 8.6\Delta_1 - 0.04A - 7.9 \quad (5)$$

Recall that L has no defined meaning in terms of absolute abundance, but is merely an index of relative numbers (see p. 816).

The relative abundance of *P. mcallii* was significantly and positively correlated with aggregate perennial density (Fig. 5). Here the correlation coefficient was 0.93. The abundance of the lizard was not significantly correlated with harvester ant abundance (Fig. 6) when all 10 plots were considered ($r = 0.47, F = 2.2, F_{0.05} = 5.1$). Although high lizard abundance indexes were generally associated with high abundances of harvester ants, Plot 5 exhibited the second highest ant index and a very low index of lizard abundance. When plots were analyzed without Plot 5 the abundance of lizards was significantly and positively correlated with the abundance of harvester ants ($r = 0.72$, $F = 7.4$, $F_{0.05} = 5.3$). Because there is no known reason to exclude Plot 5 from the analysis, we comment on this point only to suggest that some random error in sampling Plot 5 may be obscuring a real relationship.

Counts of *P. mcallii*, horned lizard scats, and nests of *Veromessor pergandei* were made at three sites east of Yuma, Arizona, in June 1980. Table 6 summarizes these observations. *Phrynosoma mcallii* was clearly more numerous in areas where nests of harvester ants (*Veromessor pergandei*) were abundant.

Discussion

Phrynosoma mcallii is not an endangered species at this time. It is difficult to find, but this has always been true (Klauber, 1939; Norris, 1949). Our work in 1979 identified a number of areas favorable for this species in Imperial and San Diego Counties (Figs. 1–4). The most remarkable of these is that lying north of Highway 78 in the vicinity of Ocotillo Wells and Benson Dry Lake (=Ocotillo Dry Lake). On two occasions, three *P. mcallii* were observed in one section in this area (Fig. 2). On 3 May, Mark Jorgensen found three *P. mcallii* impaled on creosotebush by shrikes. This area was favored by Klauber, who collected over 40 specimens of *P. mcallii* from "Benson's Dry Lake" (Reeve, 1952). It seems likely that Klauber used this name in a general sense, and that lizards were collected from surrounding areas rather than the lake bed. The region is dissected by extensive washes—particularly San Felipe Creek and Palo

Table 6. Sampling data from three areas in Arizona. Area 1 is 11–13 km southeast, Area 2 is 13–15 km east, and Area 3 is 15–23 km east of Yuma.

Area	Man-hours per km² of habitat	*P. mcallii* observed	Horned lizard scats counted	Nests of *Veromessor pergandei* counted
1	3.03	0	4	9
2	3.66	0	25	21
3	4.43	5	133	340

Verde Wash—and almost all of it lies between 50 and 100 m above sea level. The vegetation includes creosotebush, bur-sage, indigo bush, saltbush and ocotillo, and the lower portions of the landscape are exposed to flooding following heavy rains. Much of this area is embraced by the Ocotillo Wells State Vehicular Recreational Area, a 1,600-ha (4,000-ac) area administered by the Anza-Borrego Desert State Park. In addition to horned lizards recorded in the course of section searches, State Park rangers on patrols often encountered *P. mcallii* along roads.

Whitford and Bryant (1979) stated that the abundance of *Phrynosoma cornutum* in New Mexico is closely tied to the abundance of harvester ants (*Pogonomyrmex desertorum, P. rugosus* and *P. californicus*) on which it feeds. Whitford (pers. comm.) also stated that he had ". . . been able to predict horned lizard abundance in two places, Carlsbad [New Mexico] and Prescott, Arizona . . . based on density of *Pogonomyrmex* colonies . . ." The situation with *P. mcallii* is somewhat less clear, although *P. mcallii* is more dependent on ants in its diet than *P. cornutum* (Pianka and Parker, 1975: Table 6). When we estimated sizes of harvester ant colonies and combined those data with nest counts we observed a more clear-cut association between the relative abundances of horned lizards and harvester ants than shown by previous analyses. Although one or another species of harvester ants dominates the diet, *P. mcallii* may make appreciable use of smaller ants (e.g., *Conomyrma insana*). Our present view is that, although harvester ants are almost always an important component of the environment of *P. mcallii*, they are not the only one—and may not be the most important.

Whereas *P. mcallii* still exists comfortably in parts of its original geographic range, it is rapidly disappearing in others. For example, areas developed for agriculture and housing in Riverside County and in the south-central portion of Imperial County are no longer inhabited by *P. mcallii*. There are also areas along the edge of the Salton Sea, now being developed for housing, where this species probably occurred. Perhaps the most dramatic change in apparent abundance of *P. mcallii* has occurred along the 11-km stretch of California Highway 78 west of the Algodones Dunes. As pointed out previously, over 500 *P. mcallii* were captured or observed dead along this road between 1961 and 1964. But our research in 1978 and 1979 showed *P. mcallii* to be uncommon in this area. Did the collecting activity of Mayhew and his colleagues have any influence on this decline? While it is impossible to answer this question with certainty, we think not. From Mayhew's notes, we can ascertain that observations or captures of *P. mcallii* on the road were about 150 in 1961, 138 in 1962, 233 in 1963 and 41 in 1964. We do not know the collecting effort in different years, but the greatest number of lizards was observed after collecting had been carried out for two years. Certainly, numbers of horned lizards changed from year to year owing to natural events—just as we have documented for other iguanid lizards in southern Nevada (Turner, 1977: 169–171). During 1964 Mayhew commented that *P. mcallii* was less numerous than in previous years, but this was a generally poor year over most of the southeastern deserts (French et al., 1974; Turner, 1977: 172). Winter rainfall at Brawley (taken as the November, December and January total) was 16.8 mm (1960–1), 39.1 mm (1961–2), 25.9 mm (1962–3) and 8.1 mm (1963–4), so the low numbers of horned lizards observed in 1964 seem more attributable to weather than other factors. It is possible that we are dealing with historical changes in the abundance of *P. mcallii* (i.e., long-term trends rather than simple year-to-year fluctuations), but this possibility is exceedingly difficult to evaluate.

While it will never be possible to prove causes of past changes, we believe it prudent to assume that human activities are in some way implicated. Steps should be taken to protect remaining optimal habitats of *P. mcallii*. T. A. Rado (pers. comm.) has prepared an exhaustive analysis of how present and projected land use in southeastern California impinges on habitats of *Phrynosoma mcallii*. Rado showed that about 52% of the estimated geographic range of the species in California (~7,000 km²) is within areas subjected to one or more use-oriented activities (e.g., agriculture, sand and gravel quarries, off-road vehicle "open areas," prospective and approved oil, gas and geothermal leases, etc). Continued expansion of human activities in deserts will unavoidably destroy or degrade natural habitats, although it may be possible to mitigate some of the most adverse impacts. Society faces important choices in coming years, choices which can affect the quality of our deserts for many decades. If land development continues unabated we will be faced with an ever expanding roster of endangered species in the deserts of southeastern California.

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LABORATORY OF BIOMEDICAL AND ENVIRONMENTAL SCIENCES, UNIVERSITY OF CALIFORNIA, LOS ANGELES, CALIFORNIA 90024 AND 5049 S. MESAVIEW DR., LAS VEGAS, NEVADA 89120. Accepted 28 May 1981.

Coupled with a high assimilation efficiency (Dimmitt and Ruibal 1980b), this feeding ability allows it to potentially consume in one night the energy reserves for more than 1 year. Alate termites which constitute the major portion of the diet of *S. couchii* (Whitaker et al. 1977), emerge with the same summer rains that elicit emergence in *S. couchii* (Dimmitt and Ruibal 1980b). Alate termites have the highest lipid content by live weight of > 200 insect species reported in the literature (Fast 1964, Basalingappa 1970), and they are more digestible (less sclerotized) than most insects, so they probably represent a significant proportion of the energy intake of *S. couchii*. The movement ecology and potential for colonization of *S. couchii* is unknown.

Habitat: Couch's spadefoot requires temporary desert rainpools with water temperatures ≥ 15°C (Zweifel 1968) in which to breed that last at least 7 days in order to metamorphose successfully (Mayhew 1965a). Subterranean refuge sites (with a loose-enough substrate to permit burial) must occur in the vicinity of rainpool depressions where reproduction takes place. An insect food base that probably includes alate termites must be available, which implies that minimal primary production must be available to sustain this food base.

Status: Special Concern; *S. couchii* has a very small range in California and seems to be declining in other states where it is found (J. Platz, pers. comm.). In fact, ponds created by road maintenance along Hwy 78 in eastern Imperial County have actually created breeding habitat for this toad (Dimmitt 1977). Its apparent tolerance for agricultural habitat modification appears to have allowed it to persist throughout most of its historical range in California. Despite an ability to tolerate certain types of disturbance, its subterranean refuge sites may be susceptible to disturbance from off-road vehicles that create noise similar to rainfall, inducing emergence under highly unfavorable (hot, dry) conditions that would be almost certainly fatal to adults (Brattstrom and Bondello 1979). The breeding sites of this species are potentially vulnerable to disturbance that alters the percolation characteristics of the substrate in a manner that makes pools too short-lived for larvae to attain metamorphosis.

Management Recommendations: Better morphological and genetic characterization of *S. couchii* is needed to determine whether more than one taxon is represented by this species, as well as identifying which taxon may be represented in California. While the energetics of *S. couchii* are reasonably well known, it is not clear at what level trends toward increasing xerification may ultimately affect this species. In particular, it is thought that *S. couchii* may be able to accumulate enough reserves to survive two rainless summers, but how frequently this may occur or how much more depletion of its energy reserves *S. couchii* may be able to tolerate is unknown. Such data and that on its movement ecology and colonization abilities are especially needed to formulate sound management guidelines. Rigorous field testing of the noise effects of off-road vehicles is needed to assess the potential importance of this impact. *Scaphiopus couchii* utilizes a significant number of pools that were created as the result of highway or railroad construction, but many of these pools are subject to washing out, getting leaky because of disturbance of the underlying substrate, or being eliminated by culverts (S. Morey, pers. comm.). Data on the contribution of these artificial pools when compared to natural pools of various sizes (such as at the base of the Algodones Dunes) is significant for the long-term management of this species. The substrate characteristics of pools suitable for this species, particularly with regard to percolation, need study.