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## Shifts in the Relative Abundance of Snakes in a Desert Grassland

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**ABSTRACT.**— Distribution, diversity and relative abundance of snake species on roads through desert grasslands in Arizona and New Mexico were compared to data in a previously published survey conducted about 30 years ago. We found a significant shift in the relative abundance of snake species: *Thamnophis marcianus* and *Crotalus atrox* have increased in relative abundance and *C. scutulatus* has decreased. These changes are correlated with succession of local Semidesert Grasslands to Chihuahuan Desertscrub. Analysis of distributions of *Crotalus* revealed that *C. atrox* was more common than *C. scutulatus* in scrub habitat while *C. scutulatus* was more common in the remaining grasslands.

Recent studies have documented changes in squamate populations over time. Documented changes included shifts in the relative abundances of species in a community (Parker and Brown, 1973; Degenhardt, 1974; Milstead, 1974; Scudday, 1974; Brown and Parker, 1982; Fitch, 1982; Pianka, 1986), or local species extirpations and consequently modified distributions (see Lowe et al., 1986 for examples; Bock et al., 1990). Causative agents in these changes were identified as results of human activities, climatic changes, and vegetational succession.

As the characteristic vegetation of an area changes, concomitant changes in local animal populations might be expected. Beginning in the late 19th century, the desert grasslands of the southwestern United States have been invaded by mesquite and other woody shrubs (Hastings and Turner, 1965; Humphrey, 1987). Grassland animal assemblages change in response to scrub invasion (Bock et al., 1986) but specific herpetofaunal responses to vegetational transitions in desert grasslands have been little-studied (Pough, 1966; see Bock et al., 1990 for review).

We compared relative abundance of snake species in New Mexico and Arizona to data from surveys at the same site conducted about 30 years ago (1959–1961; Pough, 1966). We also examined habitat associations of *Crotalus atrox* and *C. scutulatus*. We document shifts in relative abundance of several common snake species and

correlate them with the regional history of a vegetational transition from desert grassland to desertscrub.

### STUDY AREA

We directed our efforts in the same study area surveyed by Pough (1966). The study site includes the San Bernardino Valley and part of the San Simon Valley in the southeastern and southwestern corners of Arizona (Cochise County) and New Mexico (Hidalgo Co.), respectively, at about 1300 m elevation. The site is contained by the Peloncillo Mountains to the east and predominately by the Chiricahua Mountains to the west (Fig. 1).

We used U.S. Highway 80 (U.S. Hwy 80) as a collecting transect in the valleys, and that section of Portal Road east of the American Museum of Natural History's Southwestern Research Station (SWRS) in the Chiricahua Mountains.

The vegetation of the study area during our survey was a mosaic of scrub and grasslands (Fig. 1). The Chihuahuan Desertscrub (sensu Brown, 1982a) was dominated locally by mesquite (*Prosopis* spp.), creosote-bush (*Larrea tridentata*), tar-bush (*Flourensia cernua*), white-thorn acacia (*Acacia constricta*), and wait-a-minute bush (*Mimosa biuncifera*). The Semidesert Grassland (sensu Brown, 1982b) was dominated by tobosa grass (*Hilaria mutica*) with some, usually scattered, soaptree yucca (*Yucca elata*). The area surrounding Rodeo, New Mexico was actively cultivated. The foothills of the bordering mountain ranges were predominantly Chihuahuan Desertscrub and graded into the valley floor vegetation types. The higher elevations of Portal Rd, through Cave Creek Canyon, were largely mixed riparian habitat (Pough, 1966) of montane nature and origin.

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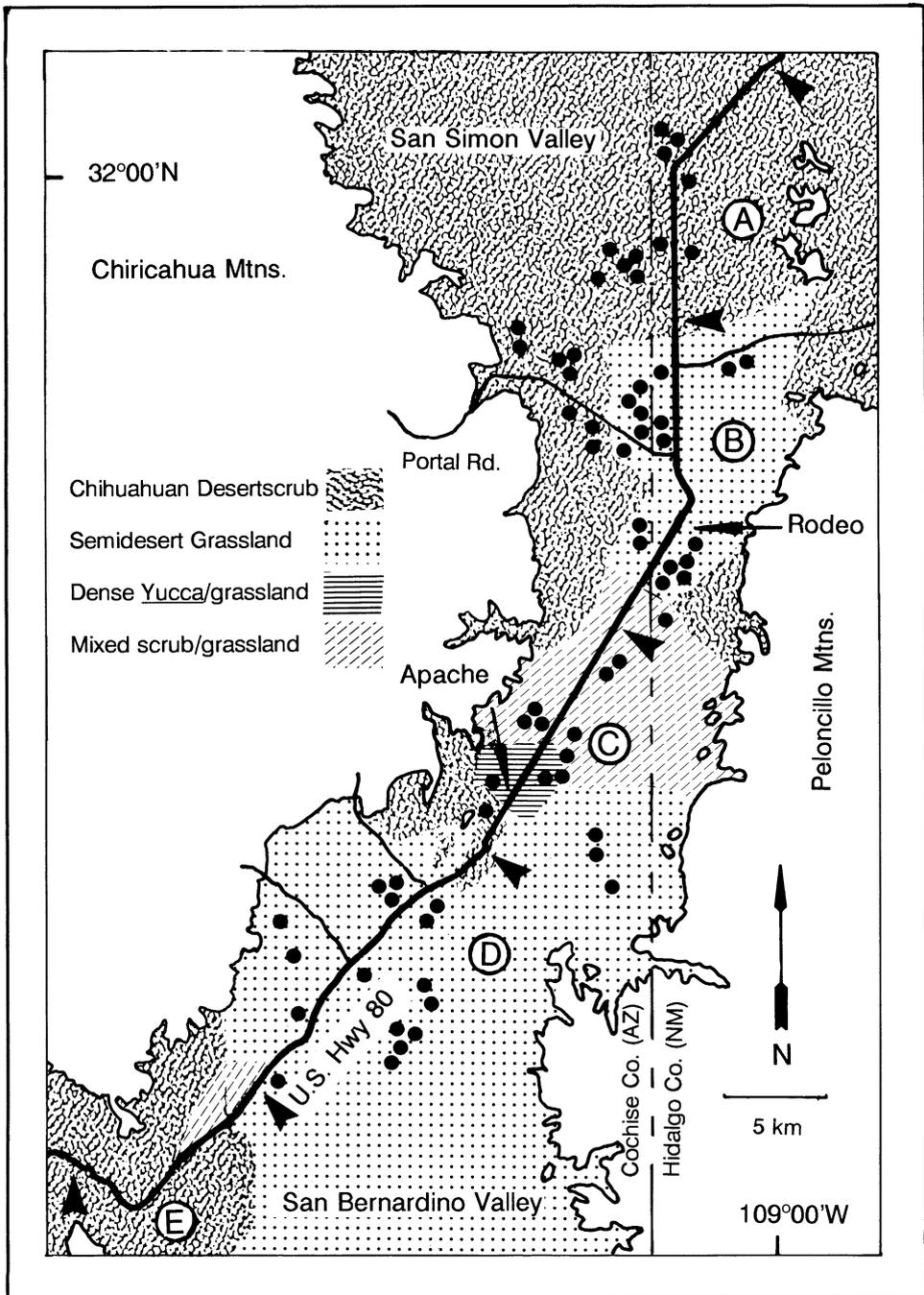


FIG. 1. Vegetation of the study area below the 1524 m contour in 1989. Eastern boundaries of vegetation types are approximate. Dots represent cattle tanks. Road sections A-E (see Methods) on U.S. Hwy 80 are indicated by arrowheads.

METHODS

The species, locality, and condition (alive, AOR; dead, DOR) of all snakes observed after dark (ca. 1930 hr) on Portal Rd (between SWRS

and its junction with U.S. Hwy 80) and on U.S. Hwy 80 (between crest of Granite Gap and Cazador Station) were recorded. Localities were taken to the nearest 0.1 mi (later converted to

TABLE 1. Comparison of effort and general results of surveys of snakes found after dark on Portal Road and U.S. Highway 80 in 1959–1961 and 1987 and 1989 (adjusted data). Totals in parentheses. (1959–1961 data from Pough, 1966).

	1959–1961		1987, 1989	
	Portal Road	U.S. Hwy 80	Portal Road	U.S. Hwy 80
Distance (km)	4448	5842 (10,290)	1997	1681 (3678)
No. species	11	11 (14)	18	17 (21)
No. individuals	114	162 (276)	82	162 (244)
Snakes/km	0.026	0.028 (0.027)	0.041	0.096 (0.066)

km) using car odometers from standardized landmarks. Each night typically began at SWRS, passed over Portal Rd twice (1 trip) and either the northern or southern section of U.S. Hwy 80 twice (1 trip). Slightly different itineraries were occasionally followed. Trips usually ended between 2300–2400 h. We collected data between 21 July and 22 September in 1987 and 1989 under a variety of weather conditions. We believe this closely approximates the methodology of Pough (1966). Vegetation was mapped (by WBJ) within ca. 1 km of the roadside along both roads in August of 1989.

We compared our raw data with Pough's (1966) using  $R \times C$  tests of independence (Sokol and Rohlf, 1981). For each road we compared numbers of all snake species observed in each survey, numbers of *Crotalus* spp. alone, and numbers of the species other than *Crotalus* spp. alone. As the latter two tests reanalyze data used in the first test, alpha was reduced from 0.05 to 0.025 for these analyses. Species not recorded in both surveys were excluded from these analyses, as were records of primarily diurnal species of the genera *Masticophis* and *Salvadora*.

Pough's surveys were made between 17 June and 26 August (F. H. Pough, in litt.). To account for the incomplete seasonal overlap of the two surveys we excluded our records after 26 August (hereafter referred to as our "adjusted" data), but retained all of Pough's (1966) data in the analyses. We present our entire data set in this paper to encourage subsequent comparisons (sensu Vitt, 1987).

We divided U.S. Hwy 80 into five equal sections on the basis of predominant local vegetation (Fig. 1) and compared *Crotalus* records ( $R \times C$  test of independence; Runs test for dichotomized data; Sokol and Rohlf, 1981) from each in order to analyze habitat separation of *C. atrox* and *C. scutulatus*. We used our unadjusted data in this non-comparative test.

Road driving may not accurately measure the abundance, or even presence, of all species in an area (Dodd et al., 1989). We feel it is an appropriate technique, however, for comparing

relative abundances of the same species over time.

All salvageable dead specimens and representative voucher specimens are deposited in the Vertebrate Museum of the University of California at Santa Barbara.

#### RESULTS

We surveyed 2857 km (67 trips) on Portal Rd and 3404 km (49 trips) on U.S. Hwy 80. We observed 320 snakes representing 23 species. Our adjusted survey effort (see Methods) and general results are compared with Pough's (1966) in Table 1. Ratios of DOR/AOR snakes were 0.43 (Portal Rd) and 0.63 (U.S. Hwy 80). On Portal Rd the most common snake was *Pituophis melanoleucus* (20.3% of all snakes). *Crotalus atrox* was the most common rattlesnake (15.9% of all snakes) on Portal Rd. On U.S. Hwy 80, *C. scutulatus* was the most common snake (23.6% of all snakes) and *Thamnophis marcianus* (16.5% of all snakes) was the most common species other than rattlesnakes. Our full data set is presented in Table 2; adjusted counts used in the comparison with Pough (1966) are included.

Comparison of our adjusted data set to Pough's (1966) results (Table 2) revealed different relative frequencies of species on Portal Rd ( $G = 33.53$ ,  $df = 8$ ,  $P < 0.001$ ). *Crotalus atrox* was more common than *C. scutulatus* on Portal Rd in our survey (50.0% of all *Crotalus* vs. 23.5%, respectively). This is different than Pough's (1966) survey (22.6% vs. 69.0%, respectively;  $G = 20.62$ ,  $df = 2$ ,  $P < 0.001$ ). Among the species other than *Crotalus* there was no difference between the two surveys for Portal Rd ( $G = 6.96$ ,  $df = 5$ ,  $P > 0.025$ ).

On U.S. Hwy 80, the overall snake species frequency in our survey was different ( $G = 47.72$ ,  $df = 10$ ,  $P < 0.001$ ) than Pough (1966) reported. *Crotalus atrox* was slightly more common than *C. scutulatus* in our survey (50.7% of all *Crotalus*, vs. 49.3%). This ratio is different than Pough's (1966) survey (25.5% vs. 74.4%, respectively;  $G = 10.87$ ,  $df = 1$ ,  $P < 0.001$ ). The relative frequency of species other than rattlesnakes was

TABLE 2. Comparison between surveys of snakes found after dark on Portal Road and U.S. Highway 80 in 1959–1961 and 1987 and 1989 (1959–1961 data from Pough 1966; Tables 1, 2). Total number of individuals followed by percentage of total in parentheses. 1987, 1989 adjusted data (see Methods) in brackets.

Species	Portal Road		U.S. Highway 80	
	1959–1961	1987, 1989	1959–1961	1987, 1989
<b>Viperidae</b>				
<i>Crotalus atrox</i>	19 (16.8)	22 (15.9) [17]	23 (14.2)	37 (20.3) [37]
<i>C. scutulatus</i>	58 (50.1)	13 (9.4) [8]	67 (41.4)	43 (23.6) [36]
<i>C. molossus</i>	7 (6.1)	12 (8.7) [9]	0	0
<i>C. lepidus</i>	0	1 (0.7)	0	0
<i>Sistrurus catenatus</i>	0	0	0	1 (0.5) [1]
<b>Colubridae</b>				
<i>Arizona elegans</i>	9 (7.9)	2 (1.4)	16 (9.9)	3 (1.6) [3]
<i>Diadophis punctatus</i>	0	1 (0.7) [1]	0	1 (0.5)
<i>Gyalopion canum</i>	0	1 (0.7) [1]	1 (0.6)	2 (1.1) [2]
<i>Heterodon nasicus</i>	1 (0.9)	0	2 (1.2)	3 (1.6) [2]
<i>Hypsiglena torquata</i>	1 (0.9)	10 (7.2) [7]	3 (1.9)	4 (2.2) [4]
<i>Lampropeltis getulus</i>	0	2 (1.4) [1]	8 (4.9)	12 (6.6) [10]
<i>L. pyromelana</i>	0	1 (0.7) [1]	0	0
<i>Pituophis melanoleucus</i>	11 (9.6)	28 (20.3) [6]	28 (17.3)	26 (14.3) [20]
<i>Rhinocheilus lecontei</i>	4 (3.5)	9 (6.5) [6]	8 (4.9)	7 (3.8) [5]
<i>Senticolis triaspis</i>	1 (0.9)	2 (1.4) [1]	0	0
<i>Tantilla nigriceps</i>	0	4 (2.9) [3]	0	3 (1.6) [3]
<i>T. yaquia</i>	0	1 (0.7)	0	0
<i>Thamnophis cyrtopsis</i>	1 (0.9)	1 (0.7) [1]	0	6 (3.3) [6]
<i>T. marcianus</i>	0	1 (0.7) [1]	3 (1.9)	30 (16.5) [29]
<i>Trimorphodon biscutatus</i>	2 (1.7)	9 (6.5) [4]	3 (1.9)	1 (0.5) [1]
<b>Elapidae</b>				
<i>Micruroides euryxanthus</i>	0	7 (5.1) [5]	0	1 (0.5) [1]
<b>Leptotyphlopidae</b>				
<i>Leptotyphlops dulcis</i>	0	9 (6.5) [9]	0	1 (0.5) [1]
<i>L. humilis</i>	0	2 (1.4) [2]	0	1 (0.5) [1]
<b>Total</b>	<b>113</b>	<b>138 [82]</b>	<b>162</b>	<b>182 [162]</b>

different on U.S. Hwy 80 ( $G = 35.09$ ,  $df = 8$ ,  $P < 0.001$ ), largely due to a much higher frequency of *Thamnophis marcianus* (38.2% of all snakes vs. 4.2%) and lower frequency of *Arizona elegans* (4.0% of all snakes vs. 22.2%) in our survey.

In our survey *Crotalus atrox* and *C. scutulatus* were differentially distributed among and within the road sections of U.S. Hwy 80 ( $G = 18.88$ ,  $df = 4$ ,  $P < 0.001$ ). *Crotalus atrox* was more common in the sections through scrub habitat whereas *C. scutulatus* was more common in the grasslands and mixed vegetation section (Fig. 2). Runs analysis (Sokol and Rohlf, 1981) revealed nonrandom patterns of distribution in sections A, C, and D. Sections B and E could not be analyzed due to small sample sizes, but the trends are clear (Fig. 2). In section D, six of the eight *C. atrox* and no *C. scutulatus* were found within the area of mesquite growth at the northern end of that section (see Fig. 1).

Fig. 3 shows the degree of scrub invasion

along Portal Rd since Pough's (1966) survey. The "*Ephedra savanna*" described by Pough (1966; his Fig. 3) barely remains. Note that we classified tarbush as *Flourensia cernua* (Compositae, as per Kearney and Peebles, 1951) and not as *Acacia constricta* (white-thorn acacia, Leguminosae, Pough, 1966). Nevertheless, both species are dominant constituents of Chihuahuan Desertscrub and clear distinctions are possible between Pough's (1966) *Ephedra savanna* (=Semidesert Grassland of Brown, 1982a) and the Chihuahuan Desertscrub.

On Portal Rd, we found no *C. scutulatus* and 6 *C. atrox* in the scrub west of Portal; 12 *C. atrox* and 7 *C. scutulatus* in the scrub habitat within 5 km east of Portal; and more *C. scutulatus* (6) than *C. atrox* (1) in the grass/scrub mosaic beyond 5 km east of Portal. This is the same pattern described by Pough (1966), although he found only *C. molossus* west of Portal.

The distribution of *T. marcianus* along U.S. Highway 80 roughly followed the distribution

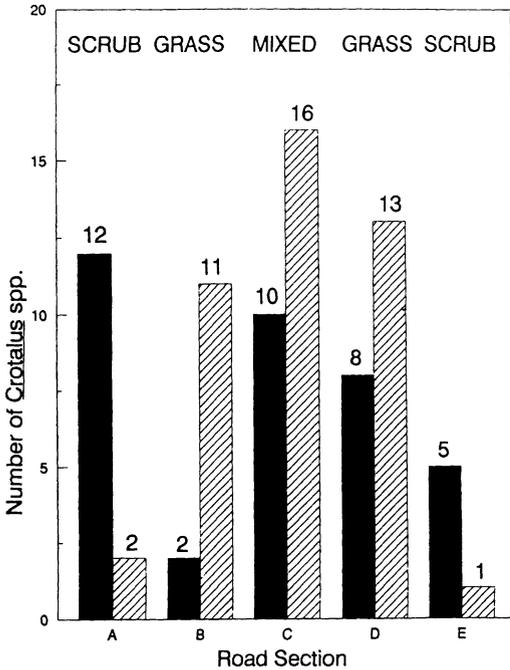


FIG. 2. Distribution of *Crotalus atrox* (solid) and *C. scutulatus* (hatched) among road sections of U.S. Hwy 80. Predominant habitat type is shown above each section. In section D, 6 of the 8 *C. atrox* records were clustered in a patch of scrub habitat at the northern end of the section; no *C. scutulatus* records came from this area.

of cattle tanks (see Fig. 1). We encountered 3, 10, 9, 6, and 2 *T. marcianus* in road sections A-E, respectively.

#### DISCUSSION

There has been a shift in the relative abundance of snake species in the San Simon and San Bernardino valleys since Pough's 1966 survey. *Crotalus atrox* now appears more abundant than *C. scutulatus*, and *T. marcianus* has become much more abundant. To establish that these differences are real, we here consider potentially confounding factors in our comparison.

Summer snake activity in this region depends largely on summer rain patterns (Reynolds, 1982), yet average seasonal rainfall (June–September) at San Simon, Arizona for 1958–1961 and 1986–1989 were very similar: 14.93 cm vs. 15.48 cm (U.S. Dept. of Commerce, 1958–1961, 1986–1989). We included the year previous to the start of each survey because prior rainfall may influence prey populations and recruitment in subsequent years.

We adjusted our data to ensure that late summer emergence of hatchling and newborn snakes did not bias the comparison. By retaining Pough's (1966) entire data set, our analysis

is conservative in that Pough's data include early summer records which we lack. Only two species (*C. scutulatus*, *Arizona elegans*), however, appear in higher frequencies in his survey. June is a dry month in this area and snake activity is minimal (B. Tomberlin, pers. comm.). Thus overlap between surveys occurs after the onset of summer rains and during the time of peak snake activity.

Road traffic volume on U.S. Hwy 80 has fluctuated greatly since 1961 (T. Hammel, Arizona Dept. Trans., pers. comm). Traffic volume in 1987 was comparable to 1959–1961 levels but in 1989 traffic increased to the highest volume recorded (Arizona Dept. Trans. data, 1961, 1989). Species have different probabilities of being killed by cars, and road traffic may affect roadside populations (Fitch, 1982; Seigel, 1986; Dodd et al., 1989). Increased traffic volume will produce more DOR snakes and thus increase the number of snakes counted. However, it should not affect the relative frequency of two behaviorally similar species such as *C. atrox* and *C. scutulatus* (DOR/AOR ratio in our study was approx 1:2 for both species). For *T. marcianus*, 35% of our records were AOR, far more than Pough (1966) recorded. Some of our records for rare species were recorded as DORs (e.g., *Heterodon*, *Gyalopion*) but most records unique to our survey were AOR (e.g., *Micruroides*, *Tantilla*).

Invasion of Semidesert Grassland by Chihuahuan Desertscrub is a widely documented trend in the southwestern U.S. (Hastings and Turner, 1965; Humphrey, 1958, 1962, 1987). We have direct (Fig. 3) and indirect (Fig. 1) evidence of this phenomenon in our study area. We have shown that *Crotalus atrox* and *C. scutulatus* have reversed in relative abundance in the study area. This is consistent with the regional vegetational trends and with the typical habitat associations of these species (Humphrey, 1936; Klauber, 1972; Reynolds and Scott, 1982; this study). These species were probably largely separated into the scrub/foothill and grassland/valley habitats at one time. As desertscrub invades the valleys, *C. atrox* replaces *C. scutulatus* in these areas. *Crotalus molossus* is largely restricted to the montane habitats and seems unaffected by these community changes.

Pough (1966) also recognized a probable prior separation of *Crotalus* species in the area but suggested that *C. scutulatus* is more arid-adapted, replacing *C. atrox* as the valleys came more to resemble "arid desert and semidesert conditions" (p. 682), referring to the expanding scrub habitat. This argument is consistent with Pough's (1966) findings of a relatively larger population of *C. scutulatus* although not with the typical habitat association of this species. It appears that Pough (1966) observed this rattle-

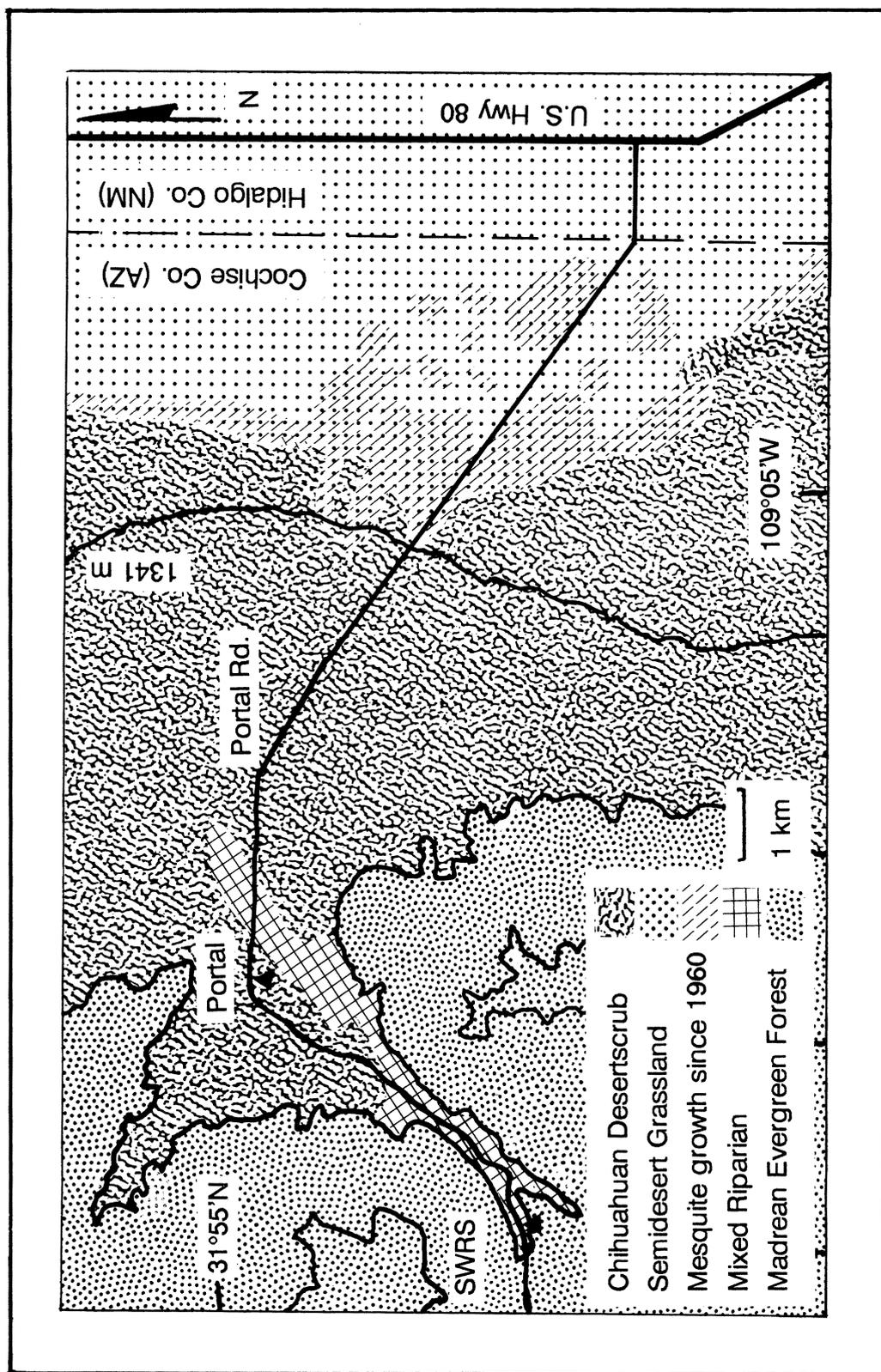


FIG. 3. Vegetation along Portal Road in 1960 with additional mesquite growth noted in 1989. 1960 data modified after Pough, 1966 (see text).

snake community in a situation more similar to its pre-disturbed condition.

*Arizona elegans*, *Sistrurus catenatus* and *C. viridis*, all known from the area, are now rare or locally extirpated (Lowe et al., 1986; this study). These are grassland species whose rarity we attribute to decline of grassland habitat. Pough (1966) recorded neither rattlesnake, so we cannot postulate their previous abundance nor a time frame for their decline. Generalist species (e.g., *P. melanoleucus*, *Lampropeltis getulus*) have shown little change since 1959-1961.

We attribute the increase in *T. marcianus* to human factors. This species feeds primarily on larval and metamorphosed anurans, especially *Bufo* spp. and *Scaphiopus* spp. (Fouquette, 1954; pers. obs.) which were abundant in the cattle tanks (Fig. 1) during our survey, and *Rana catesbeiana* in other areas (R. A. Seigel, in litt.). *Thamnophis marcianus* is apparently expanding its range, following human water development of arid areas (Stebbins, 1966; Shaw and Campbell, 1974), as have certain desert toads (Sullivan, 1986).

We recorded nine snake species not reported by Pough (1966). We do not believe that these species were absent from the area during Pough's (1966) survey. These are small and secretive species and most of our records were from the scrub habitat. Areal increase of scrub habitat may have contributed to their proliferation, such that they are now detectable in a road survey. Differences between the two surveys in sampling for small species may also account for these differences.

Even in historical times, the Semidesert Grasslands of the southwest were not uniform in character like the Great Plains (Hastings and Turner, 1965). Habitat changes in the region consist of expansion and decline of the plant communities already present in the mosaic. We have documented concomitant changes in the populations of snake species associated with these plant communities.

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