

Biology Of Whiptail Lizards (Genus *Cnemidophorus*)

Editors

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**A PUBLICATION OF THE
OKLAHOMA MUSEUM OF NATURAL HISTORY
AND
THE UNIVERSITY OF OKLAHOMA**



HERPETOLOGISTS' LEAGUE SPECIAL PUBLICATION NO. 3

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Cite as: Wright, J. W., and L. J. Vitt. 1993. Biology of Whiptail Lizards (Genus *Cnemidophorus*). Oklahoma Mus. Nat. Hist., Norman, Oklahoma, USA

Production managed by Laurie J. Vitt
Computer expertise provided by Cameron Kacmarcik
Printed and bound by Printing Services of the University of Oklahoma

ISBN 1-883090-01-6

Oklahoma Museum of Natural History, Norman, Oklahoma 73019

Chapter 13

Community Ecology Of *Cnemidophorus* Lizards In Southwestern Texas: A Test Of The Weed Hypothesis

JOS. J. SCHALL

A remarkable species richness of *Cnemidophorus*, or whiptail lizards, exists in the Chihuahuan desert of southwestern Texas. Nine species occur in the region between the Pecos river and Rio Grande (the "Trans-Pecos"), and up to four, in various combinations, can coexist at the same site. Seven of these occurred on my study sites. They are: *C. gularis*, *C. septemvittatus*, *C. tigris*, *C. inornatus*, *C. exsanguis*, *C. tessellatus*, and *C. dixonii*. The last three species are parthenogenetic. This assemblage of species, and similar less diverse ones in other parts of the American southwest, have long intrigued ecologists. How do these species coexist when they appear similar in body form as well as in food and habitat preference? Case (1983) stated that *Cnemidophorus* are distinct from all other U.S. lizards in foraging behavior and overall ecology and thus form a "guild" of species that can be examined independently of other lizards. Is there an ecological "limiting similarity" (MacArthur and Levins, 1967) among these species by which they partition resources to reduce potential competition?

Lizards have long been important models in studies of resource partitioning (Pianka, 1986). Classic works include Barbault (1974) on *Mabuya*, Schoener (1968) on *Anolis*, Pianka (1969) on *Ctenotus*, Hillman (1969) on *Ameiva*, and Pianka and Pianka (1976) on *Diplodactylus*. In all of these congeneric assemblages there were important differences among species in habitats used, times of activity, and taxa and size of prey eaten. William Milstead was the first to study seriously the *Cnemidophorus* of southwestern Texas (1957a, 1957b). The relatively undeveloped taxonomy of the genus at that time led Milstead to confuse several species and believe he was working with only four taxa. He concluded that all the species occupied the same niche, but could not coexist permanently at the same location. That is, "...no species has an advantage that will allow it to displace another species." Milstead emphasized historical factors such as time of arrival of each species at a site in determining the composition of the assemblage. Scudday (1971) reexamined this assemblage and concluded that the species were subject to "cyclic sympatry" in which species compo-

sition was unstable. These views suggest the Trans-Pecos whiptail community is an unstable one, never reaching an equilibrium, competitive stage.

Other *Cnemidophorus* groups have been studied in the southwestern US. Results were similar to those reported by Milstead. Medica (1967) examined four species in New Mexico. Foods eaten overlapped by 90% (based on taxa, my calculation of overlap from his raw data table), and all four species were found at some sites. Echternacht (1967) studied two species in Arizona and concluded they "occupy very similar, but not identical, ecological niches." Food overlap was very high (mostly termites), but foraging behavior differed somewhat between the two species. Case (1983) proposed that body size is important in determining which whiptail species can coexist. In the Gulf of California region two species commonly exist at a site, but these are always different in body size (this picture is reminiscent of the pattern in body size of *Anolis* on Caribbean islands [Schall, 1992]). *Cnemidophorus tigris* is often one species in a pair but varies greatly in body size; in some locations it is the small species in the pair, and in others it is the larger species. Case also examined body size of coexisting species at sites in Texas, including the Trans-Pecos region. His results suggest that body size is also important in the more complex assemblage of *Cnemidophorus*, but my reanalysis disputes this (below).

In summary, the kind of resource partitioning found in other assemblages of congeneric lizards has not been found in the whiptail communities. Thus, there is a "paradox of the lizards" to rephrase Hutchinson's (1961) classic title. How do these species coexist without suffering severe competition?

As mentioned above, some of the *Cnemidophorus* in the American southwestern deserts are parthenogenetic. Approximately a third of the ≈ 45 species of *Cnemidophorus* are known now to be all-female forms (Cole, 1975; Wright, 1978; Moritz *et al.*, 1992). Wright and Lowe (1968) presented an important hypothesis to account for the origin and distribution of these all-female whiptail species. Unisexual species are of hybrid origin, highly heterozygous, usually triploid, and are distributed in ecotonal, unstable habitats. These facts led Wright and Lowe to characterize unisexuals as animal "weeds" adapted to unstable, extreme, disturbed, or disclimax environments. Weedy species are assumed to be fugitives, colonizers, or species of early successional habitats. Such organisms prosper in transient, disturbed, nonequilibrium, or unsaturated zones where competition is slight. Weeds are ecologically flexible, and exploit a broad range of habitats and resources (broad niched). However, they are adapted to rapid exploitation of a newly opened habitat and consequently display poor competitive ability (Sakkai, 1965).

Are parthenogenetic whiptails animal “weeds” as suggested by Wright and Lowe? Areas of the southwestern U.S., including the Chihuahuan desert of Texas, have been subject to major climatic changes since the Pleistocene (Morafka 1977; Martin and Mehringer, 1965). There have been “repeated and reversible shifts in vegetation between desert scrub and semi-arid grassland (Morafka, 1977).” Thus, these species probably originated when their parental taxa were brought together by habitat alteration that allowed hybridization to occur.

Earlier I proposed two tests of the Wright and Lowe weed hypothesis (Schall, 1977, 1978, 1981). If the all-female *Cnemidophorus* are animal weeds, they should have relatively r-selected reproductive traits and have broader thermal tolerance than bisexual species. I found no differences in reproductive or body temperature characteristics between two all-female species of the Texan desert and three bisexual forms. Here I test another prediction emerging from Wright and Lowe’s hypothesis: that all-female species should have a broader range of habitats, broader use of resources, and more patchy distributions in generally disturbed zones. Niche overlap between bisexual species should be low, similar to that seen in other congeneric assemblages of lizards, but overlap of the all-female forms with all other species should be considerable. Species composition at individual sites should be unpredictable when all forms are considered, but should have patterns of exclusion when only the bisexual species are examined. Thus, the “paradox of the lizards” is resolved if the all-female species have the weedy characteristic of broad overlap with other congeners in disturbed, nonequilibrium habitats.

Study Sites, Species Studied, And Methods

I studied the five most common whiptail species, two parthenogenetic (*Cnemidophorus tessellatus* = diploid; *C. exsanguis* = triploid), and three bisexual (*C. tigris*, *C. inornatus*, and *C. gularis*). Two other species are found in the area in which I worked, but are not included here for most analyses. *C. septemvittatus* is primarily a highland relic in the United States, but distributed more widely in Mexico, and *C. dixonii* has a very limited range in Texas near the town of Presidio (Scudday, 1973). Taxonomic treatment of these species is in Scudday (1971) and color pictures of all are in Conant and Collins (1991).

Most work reported here was conducted at 45 sites in Brewster, Culberson, Jeff Davis, Pecos, Presidio, and Reeves Counties, Texas, within a range of about 2° longitude and 3° latitude (Fig. 1). Elevations ranged from 640 to 1600 m. Precise locations of the sites are available from the author. *Cnemidophorus* become active in my study region in early May and activity falls off sharply in late August. Therefore, eight months of field

work were divided over four months during each of two years. Each study site was visited on 1-16 days (half of the sites were visited at least three times) and lizard specimens were collected from all 45 sites. Not all information was collected for each individual lizard so sample sizes vary for different kinds of data.

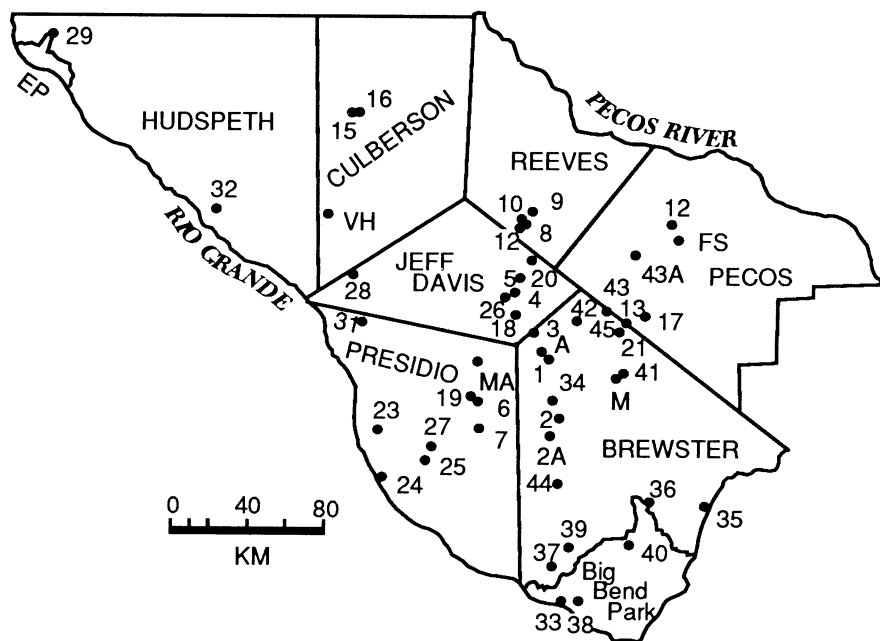


FIGURE 1. Location of study areas in Trans-Pecos region of Texas. Counties are given as well as location of Big Bend National Park. Major towns are indicated as EP = El Paso, VH = Van Horn, FS = Fort Stockton, M = Marathon, A = Alpine, and MA = Marfa.

Four niche dimensions were examined: macrohabitat, microhabitat, foods eaten, and time of activity. For most individual whiptails sighted I recorded: (1) species; (2) time of day, converted later to hours since sunrise corrected for geographic location and date; (3) behavior of the animal, especially if it was interacting with another lizard; (4) microhabitat using classes reported in Table 1. Macrohabitat type was recorded for each site (classes in Table 2). Macrohabitat describes the general structure of the site including slope, major plant associations, etc. Elevation for each site was determined from U.S. topographical maps.

Lizards were collected with 22 cal. no. 12 shot and weighed at once with a Pesola spring scale to the nearest 0.1 g. In the laboratory specimens

TABLE 1. Microhabitats used by five species of *Cnemidophorus*. Numbers are % of all lizards sighted in that class. N = total number seen, B = niche breadth, SB = standardized niche breadth. Species indicated by first two letters of their specific name. Types of microhabitats are mostly self explanatory except "roughland" which was steep, often rocky slopes or draws.

	TI	TE	GU	EX	IN
Open sun	.375	.388	.129	.295	.321
Rocks	.018	.009	.004	.081	.022
Roughland	.019	.013	0	.014	.008
Grass	.010	.167	.367	.256	.198
Edge grass	.001	.044	.117	.116	.049
In vegetation	.162	.175	.148	.053	.104
Edge vegetation	.204	.127	.212	.126	.231
Base of small isolated shrub	.198	.105	.015	.032	.068
Climbing shrub	.008	0	0	0	0
Woodland	.002	.022	.008	.031	0
B =	4.02	4.94	4.31	5.17	4.67
SB =	.40	.49	.43	.52	.47
N =	771	228	264	285	511

TABLE 2. Habitat types used by five whiptail species; number of sites of each type where each species was found is given. High grassland = higher elevation zone of broad stretch of grassland typical of high flat valleys in the Trans-Pecos; High grass - disturbed = road edges and plowed areas; woodland = wooded areas along streams, cattle tanks, or some of the highest elevation locations; grass-shrub-trees = a more vegetated, very shrubby zone, often along streams; mixed habitat = clearly ecotonal areas between grassland and desert flats; creosote flat = a large expanse of flatland desert with primarily creosote shrubs; roughland = steep rocky slopes.

Kind of Site	TI	TE	GU	EX	IN
High grassland		2	9	1	12
High grass-disturbed		1	6	8	3
Woodland	2	2	5	4	2
Grass-shrub-trees		1	5	1	2
Mixed	3	7	1	2	4
Creosote flat	13	3			3
Roughland	7	4		2	5

were sexed, and various measurements taken: snout to vent length (SVL), head length from anterior end of ear opening to tip of snout, head width at widest point, tail length from tip to vent, foreleg length and hind leg

length from posterior junction of leg and body to tip of longest toe. Relative head, tail, and leg lengths were expressed as a proportion of SVL.

Stomachs of specimens were removed and their volumes determined by water displacement in a graduated cylinder to nearest 0.05 ml. After food was removed from the stomach, the volume of the empty stomach was taken in a similar fashion to give the approximate volume of all food. Foods were separated to taxon and arranged to uniform thickness on a petri dish which had a 1 mm grid graph paper pasted underneath. This allowed an estimate of % of the stomach contents that was devoted to each food type. Length of each prey item was also measured.

Sizes of geographic distribution of whiptails and other lizard species were determined by plotting range on a map marked with 1° latitude x 1° longitude squares. The number of squares occupied by each species' distribution gave approximate range size. Distributions illustrated in Conant (1975) and Stebbins (1966) were used. Only those species which have most of their range within the United States were used because the ranges of lizards in Mexico are less well known.

The following metrics were calculated. For niche breadth I used the measure of Simpson (1949). This metric increases to i , the number of resource classes (number of food types, for example), when each resource class is used equally often. To compare niche sizes across niche dimensions (and for future possible comparison with other studies) I calculated a standardized niche breadth as: Niche breadth/number of resource classes. For niche overlap I use the measure of Pianka (1973). This is a symmetric measure that ranges from 0 for no overlap to 1.0 for complete overlap. May (1975) gives reasons why this metric is the most useful one for ecologists. Last, to measure interspecific associations based on among-site comparisons, I use the method of Hurlbert (1969) which is based on a chi-square statistic.

Results

Interference between individuals

I scored interactions between individual whiptails for 62 meetings in which I subjectively judged that the animals were close and saw one another. In 39% of these meetings I ranked the outcome as agonistic. In these, one lizard chased the other for distances ranging from a few cm to 0.5 m. In only one case did actual biting and body contact result (two *C. inornatus*). Leuck (1985) has conducted experiments showing that some species of parthenogenetic whiptails are less aggressive than some bisexual species perhaps because of the impact of kin selection. My sample sizes, however, were too small to conduct such a comparison. Hostile behavior was seen both in conspecific and interspecific meetings. This suggests that

the chasing behavior is a means of reducing competition for hidden foods being searched out at a particular patch of the habitat.

Times of activity

Animals were commonly sighted from 2 to 3 h after sunrise except on cool mornings or the day after cool or wet weather when lizards took several more hours to become active (Fig. 2). *C. exsanguis* has the shortest activity time and peaks earlier than other species. *C. inornatus*, the smallest species, has a the broad time niche and it was active even on cool mornings when other syntopic species took several more hours to begin activity. *C. tigris* has the broadest range of activity times; I have seen this species active well after dark on hot evenings.

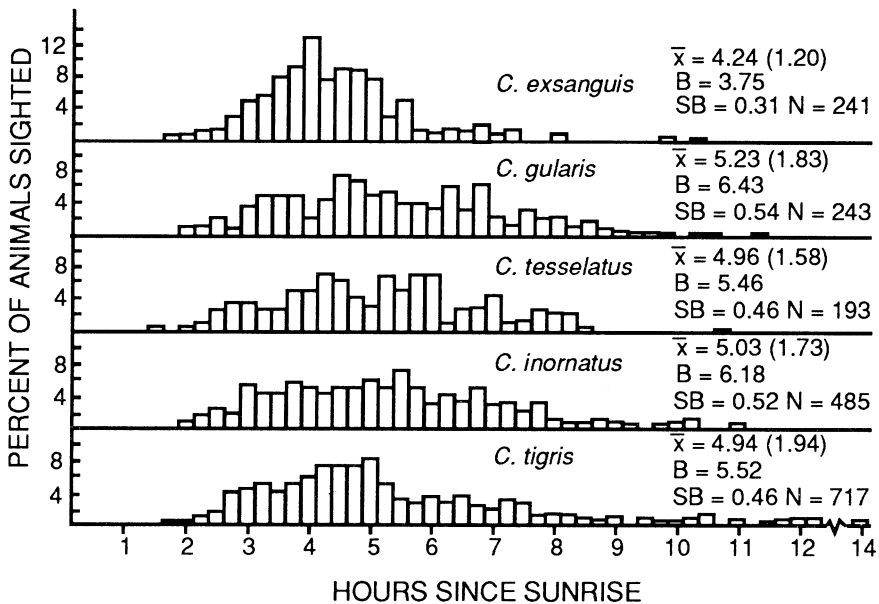


FIGURE 2. Histogram of times of activity of five species of *Cnemidophorus*. Mean, SD, sample size, time niche breadth (B), and standardized niche breadth (SB) given.

As study sites varied considerably in elevation, examination of time of activity data site-by-site is useful. At those sites where enough animals were observed, *C. inornatus* generally had broad times of activity (Time niche breadth [=B] for sites 6 and 7 was 5.0, for site 19, 5.2, and for site 14, 6.7). Likewise, *C. exsanguis* generally had shorter activity times (B = 3.1 - 4.9 for 10 sites [sites 1-5, 13, 20, 21, 26, and 31]). *C. tigris* at site 8

had a time niche breadth similar to that seen in the overall measure ($B = 5.9$). Thus, the analysis of site-by-site data are similar to the results shown in Fig. 2 for combined results.

Overlaps between species in times of activity were high, ranging from .80 to .98, and average overlap between bisexual species (.900) was similar to average overlap between the all-female species with all others (.960). I conclude that there is very little separation among species in the "time" niche dimension and there is no difference between the bisexual and all-female species in their times of activity.

Foods eaten

These lizards are opportunistic feeders and eat a very wide variety of prey types (Table 3). However, termites (*Amitermes*) are the most frequent prey of four species. Beetles, grasshoppers, and caterpillars are other important prey consumed. Contrary to the prediction emerging from the weed hypothesis that all-female species should have the broadest niches, *C. tessellatus* and *C. exsanguis* had the narrowest food niches of the five species. *C. tigris* overlaps in diet the least with other species (Table 4). Excluding this species, mean overlap in diet is very high (0.94), but even including *C. tigris*, mean overlap is considerable (0.82). Mean overlap between the three possible bisexual species pairs (.768) was similar to the seven possible pairs of an all-female species with another species (.838).

As prey availability must vary among study sites, I chose 5 sites where 2-4 species were syntopic and examined food overlaps at these locations. Overlaps within sites were usually very high (> 0.90). Thus, the lower food niche overlap of *C. tigris* (Table 4) is probably a result of this species being less often syntopic with other whiptails rather than any real difference in dietary preference. Species that often occur together (*C. gularis*, *C. exsanguis*, and *C. inornatus*) have high food niche overlaps.

Whiptails might well consume the same prey taxa, but of different sizes. There are significant differences in head lengths among the five *Cnemidophorus*, although relative head lengths are very similar (Fig. 3, Table 5). Juveniles have relatively longer heads (correlations for SVL and Head Length/SVL are all negative and significant [r 's range from -0.20 to -0.72, $P < .0001$]). Males of bisexual species also have larger heads than females (Newman-Keuls tests, $P < .05$). Such differences between sexes and among age classes might well be important in reducing both intra- and interspecific competition for food. However, as the hypothesis being examined concerns only interspecific relations, I combined all intraspecific data to compare food size and head size among the five species. Head size and size of largest food items in the stomach are correlated among species (Fig. 4). However, there is considerable overlap in prey sizes and no significant differences among the four larger species (t tests, $P > .05$). However, the

TABLE 3. Foods eaten by five species of *Cnemidophorus* in southwestern Texas. Data are % of volume. N = number of stomachs examined. Species given by first two letters of specific name.

Prey Class	TI	TE	GU	EX	IN
Termites	.130	.561	.451	.475	.430
Beetles	.162	.142	.107	.088	.074
Beetle Larvae	.045	.036	.024	.003	.015
Flies	.041	0	.005	0	.014
Grasshopper Adults	.011	.018	.027	.132	.013
Grasshopper Nymphs	.085	.027	.182	.084	.212
Lepidoptera Adults	0	.012	.003	0	.013
Lepidoptera Larvae	.168	.055	.076	.021	.019
Spider Egg Cases	.002	0	0	.009	0
Spiders	.037	.023	.030	.053	.032
Scorpions	.046	.005	.021	.004	0
Other Arachnids	.076	.013	0	.038	.007
Ants	.017	.007	.001	0	.022
Other Hymenoptera	.025	.018	.009	.002	.021
Other Orthoptera	.010	.010	.005	0	.017
Ant Lion Larvae	.012	.006	.026	.013	.002
Other Insects	.015	.014	.010	0	.053
Not Identified	.113	.047	.045	.045	.052
Stones	.006	.006	.006	.010	.004
Plant Matter	0	0	.005	0	.0002
Vertebrates	0	0	.003	.023	0
N	66	50	81	59	120

TABLE 4. Overlap matrix for foods eaten by five species of *Cnemidophorus*. Also given are niche breadths (B) and standardized niche breadths (SB). Species given by first two letters of specific name.

	TI	TE	GU	EX	IN
TE	.616				
GU	.702	.935			
EX	.589	.956	.939		
IN	.622	.911	.980	.923	
B =	9.44	2.91	4.38	3.77	4.09
SB =	.45	.14	.21	.18	.19

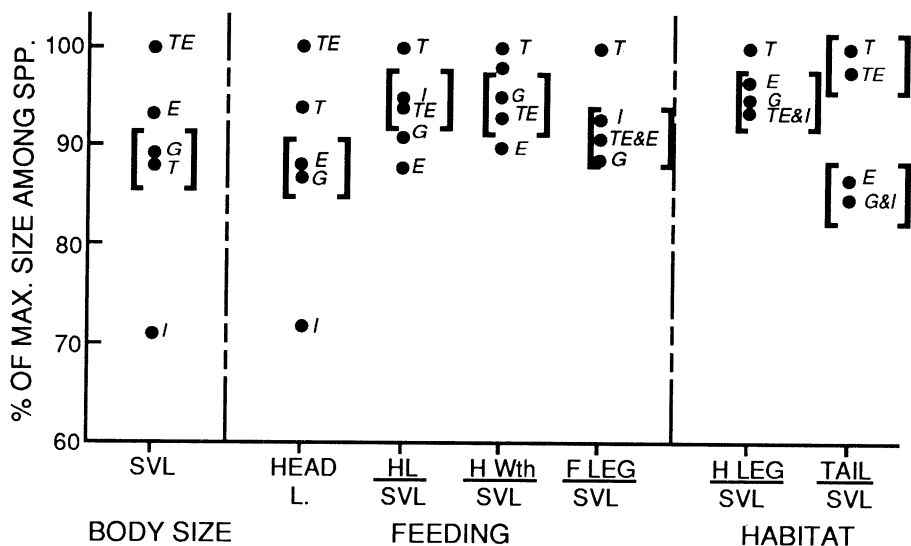


FIGURE 3. Body measurements for five species of *Cnemidophorus*. Sizes are given as a % of the maximum for each measurement for all of the five species. Thus, *C. inornatus* is the smallest lizard in snout-vent length (SVL) at about 70% that of the largest species *C. tessellatus*. Measurements of head length, head length divided by SVL, head width divided by SVL, and length of foreleg divided by SVL may be those relevant to feeding of the lizards (foreleg is used in digging up food items). Hind leg length divided by SVL and tail length divided by SVL should be related to locomotion and thus related to habitat use. Groups in brackets are those with no significant difference among them. Code is for first letter(s) of specific name: T = *C. tigris*, Te = *C. tessellatus*, I = *C. inornatus*, E = *C. exansguis*.

TABLE 5. Body size measurements for five species of *Cnemidophorus*. Species indicated by first two letters of specific name. Means, SD below mean, and sample sizes given.

	TI	E	GU	EX	IN
SVL	69.1 (9.5)	78.5 (10.6)	70.8 (10.1)	73.2 (8.2)	55.6 (4.8)
Head Length	17.0 (.14)	18.0 (.17)	15.7 (.20)	15.9 (.11)	13.0 (.07)
Sample Size	289	164	147	206	316

smallest species, *C. inornatus*, consumes significantly smaller prey than the others (t' test, $P < .01$).

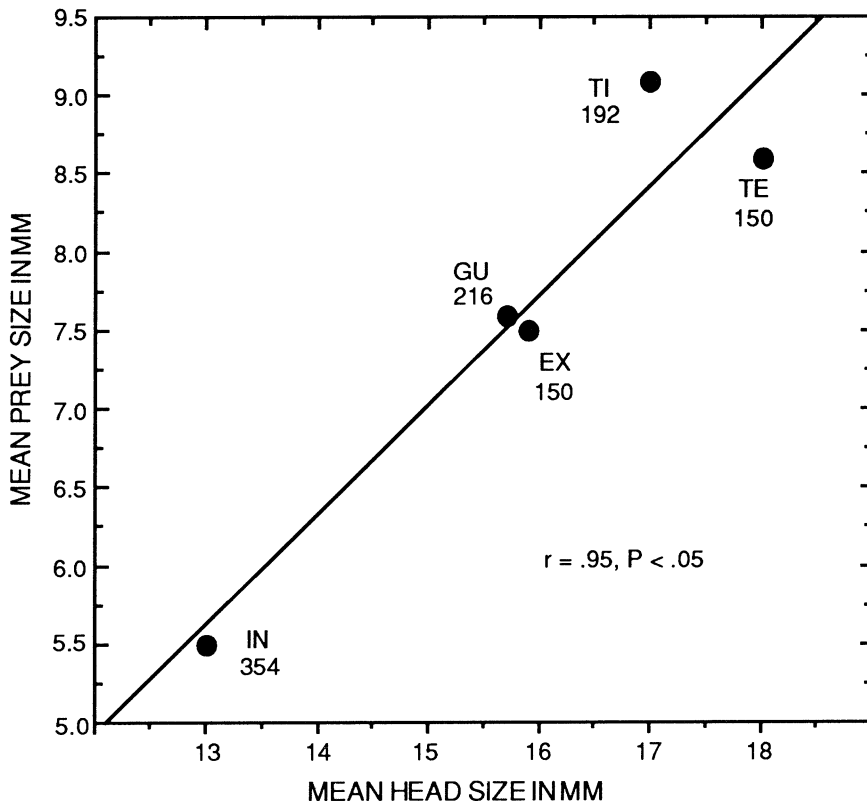


FIGURE 4. Mean head length plotted against mean size of three largest items in stomachs for five whiptail species. Species are indicated by first two letters of specific name. Numbers next to points are sample sizes of prey measured.

The prey classes are broad, so the smaller foods eaten by *C. inornatus* might well represent different species compared to the larger foods eaten by other whiptails. (This effect could also be present for the other *Cnemidophorus*, but less pronounced.) *C. inornatus*, for example, does not eat the robust beetle species often consumed by the larger whiptails. It does eat the same grasshopper species as the other whiptails, but takes smaller nymph stages (T. Joern, pers. comm.).

Whiptails could also partition food resources by foraging in somewhat different fashions; however, quantifying foraging techniques is difficult because such techniques vary by weather conditions, time of day, and study site. *Cnemidophorus* have excellent vision (Benes, 1969) and olfactory ability (Stebbins, 1948; Schall, 1990). All five of the Trans-Pecos whiptail species characteristically move through an area, periodically "nose dipping" or tapping their snout down, often touching the ground; occasionally they lick and the tongue may actually contact the ground (revealed in frame-by-frame viewing of high-speed cine films; unpubl. data). These superficial observations suggest foraging behavior is similar for all species.

In summary, all the whiptail species overlap greatly in food taxa consumed (primarily termites excavated from dead plant material), and the four largest species have no significant difference in food sizes. However, the smallest species tends to eat smaller prey. There is no clear difference in patterns of food use by the all-female and bisexual species.

Microhabitats

Ten microhabitat classes were chosen. Choice of classes is obviously subjective (how a lizard views its surroundings is conjectural), but is not random here. Earlier (Schall, 1975) I attempted to delimit objectively those habitat characteristics that determine population density in a tropical whiptail species. Here I use those conclusions, my preliminary observations on the west Texas *Cnemidophorus*, and data of other authors to arrive at microhabitat classes.

Species differ significantly in microhabitat utilization (Table 1). *C. tigris* uses open areas more frequently than any other species and the difference is significant for the *C. tigris* X *C. gularis*, *C. exsanguis*, and *C. inornatus* pairs (c^2 tests; P 's < .01 - < .005). *C. tigris* is also often at the base of creosote (*Larrea*) shrubs in desert flats. In addition, *C. tigris* has the longest hind legs and tail of the species studied (Fig. 3). These morphological traits must be important for rapid locomotion over open areas (Pianka, 1986).

Cnemidophorus gularis is similar in SVL to *C. tigris*, but utilizes grassy, more vegetated microhabitats. About half of *C. gularis* individuals were sighted in or near grass, a microhabitat *C. tigris* rarely enters. Thus, these two species may be seen as complementary forms, one in dry desert flats and the other in grassy habitats.

Except for the *C. gularis* - *C. tigris* pair, overlaps in microhabitats are high, ranging from 0.71 for *C. tigris* X *C. exsanguis* to 0.83 - 0.95 for the other species pairs. Site-by-site comparisons where sample sizes are large reveal a similar pattern. For 14 pairs at 8 sites, overlaps averaged 0.79 (range 0.60 - 0.97). However, at two sites where *C. gularis* and *C. tigris* were syntopic, overlap was 0. For example, at site 8 bordering Balmorhea

lake in Reeves county, a creosote flat met a grassy zone nearer to the lake. *C. tigris* was restricted to the creosote flat and *C. gularis* to the grass. Site 12 was nearby in Reeves county and was a creosote flat that met a grassy zone that blended into a more vegetated habitat. *C. inornatus* was in all three habitats, *C. gularis* in the grass and vegetation, and *C. tigris* in the creosote.

Comparing the bisexual and all-female species reveals that the two parthenogenetic species have the broadest microhabitat niche breadths, but mean overlaps between bisexual pairs (.737) is similar to that for all-female pairings with other species (.860).

Macrohabitats

Significant differences were found in elevation of sites (Fig. 5) among species (Kruskal-Wallis test, $P < .01$). *C. tigris* was found at significantly lower elevations where creosote flats occur compared to *C. gularis*, *C. inornatus*, and *C. exsanguis* (Mann-Whitney tests, $P < .001$). *C. exsanguis* was found at significantly higher elevations than other species. (M-W tests, $P < .01$).

Seven macrohabitat classes were distinguished (Table 2). As expected from the microhabitat data, *C. gularis* and *C. tigris* have different macrohabitat preferences. The unisexual species are found in a greater variety of zones when compared with the two larger bisexual species. For example, both *C. tessellatus* and *C. exsanguis* are found in high elevation grassy flatlands and also in lower elevation steep rocky slopes. Each parthenogenetic species, though, more closely resembles one of its bisexual parental species (*C. tigris* for *C. tessellatus*, and some population of a *C. gularis*-like lizard for *C. exsanguis*). *C. inornatus* also has a broad range of macrohabitats, but is usually found in grassy zones.

Species associations and community predictability

The Trans-Pecos region of Texas is well known for its unpredictable and harsh weather conditions as well as vegetational shifts (Morafka, 1973). Local residents related to me numerous anecdotes concerning unusual weather patterns and biotic changes. Some examples were ice storms in summer, periodic droughts (in some cases, very localized: two of my sites had received no rain at all for 14 months prior to my visits while nearby areas were quite green), and flash floods (two of my sites were devastated by massive flooding the year before my study began).

I noticed lizard community shifts in the two summers at several sites. Several examples follow: (1) At site 2 in Brewster county *C. gularis* and *C. exsanguis* were common animals during the first season of field work whereas *C. tigris* were rare. By the next year much of the grass had died back and *C. tigris* was common, and *C. exsanguis* and *C. tessellatus* were both present, though not common. (2) At Lake Balmorhea (site 8), *C.*

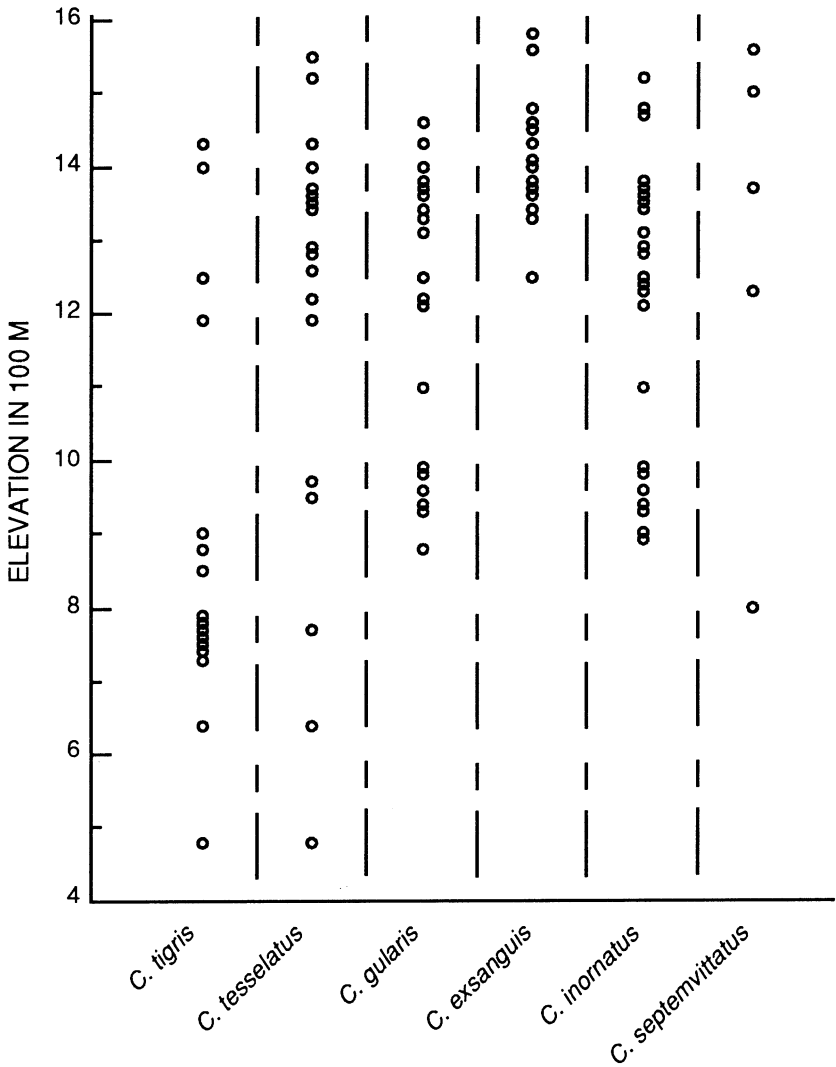


FIGURE 5. Distribution of six *Cnemidophorus* species by elevation. Each point represents a site. As more than one species usually occurred at a site, the total number of points is greater than the actual number of sites visited.

gularis was common in the grassy zone near the lake (discussed above). The next year had decreased rain, a lower lake, and die-back of grass. *C. gularis* was much less common and *C. tigris* moved into the newly dried

zone. (3) At site 26 in Jeff Davis county, *C. gularis* and *C. exsanguis* were abundant in the first season, but *C. gularis* had completely vanished the next season.

A more objective way to approach community predictability is through coefficients of interspecific association analysis (Hurlbert, 1969). For adequate analysis, this method requires a large sample size of sites because every species is not found at each site. Therefore, my results would be treated with caution (Table 6). As expected, *C. tigris* and *C. gularis* are strongly and significantly negatively associated. Likewise, *C. exsanguis*, which resembles one of its parental species, *C. gularis*, more than it does *C. tigris*, is negatively associated with *C. tigris*. *C. tessellatus*, more similar to its parental species *C. tigris*, is negatively associated with *C. gularis*. A reasonable assumption is that *C. exsanguis* and *C. tessellatus* should therefore be negatively associated; however, the unisexuals are not significantly associated suggesting their occurrence together is more-or-less random. Of 10 species pairs, only four are significant suggesting that community predictability is low except for the pairs discussed above.

TABLE 6. Coefficients of interspecific association. Numbers in bold face are significant at $P < .005$. Metric ranges from - 1.0 for negatively associated species to + 1.0 for positively associated species.

	<i>C. tigris</i>	<i>C. tessellatus</i>	<i>C. gularis</i>	<i>C. exsanguis</i>
<i>C. tessellatus</i>	.38			
<i>C. gularis</i>	-.89	-.75		
<i>C. exsanguis</i>	-.84	-.13	.44	
<i>C. inornatus</i>	-.30	.11	.07	-.37

Case (1983) examined body size of coexisting species at sites in Texas, most of which were in the Trans-Pecos region (Fig. 14.12, p. 324 in his paper). He found a surplus of dissimilarly sized pairs than expected by chance and concluded that size is important in structuring the whiptail assemblages. Fig. 6 contains the number of species found at my study sites; the most common situation consisted of two syntopic species. I constructed a graph based on Case's format for sites with two species (Fig. 7); not enough sites with triplets were available for a similar analysis. At 12 sites the pairs were more different in body size than the mode, and at 12 sites the pairs were less different than the modal size difference. The major difference between Case's result and mine (Fig. 7) is that the most common pair in this study was *exsanguis-gularis*, whereas Case had no site with this pair of species. I conclude that there is no evidence of overall effect of body size on determining coexistence of species pairs in this assemblage.

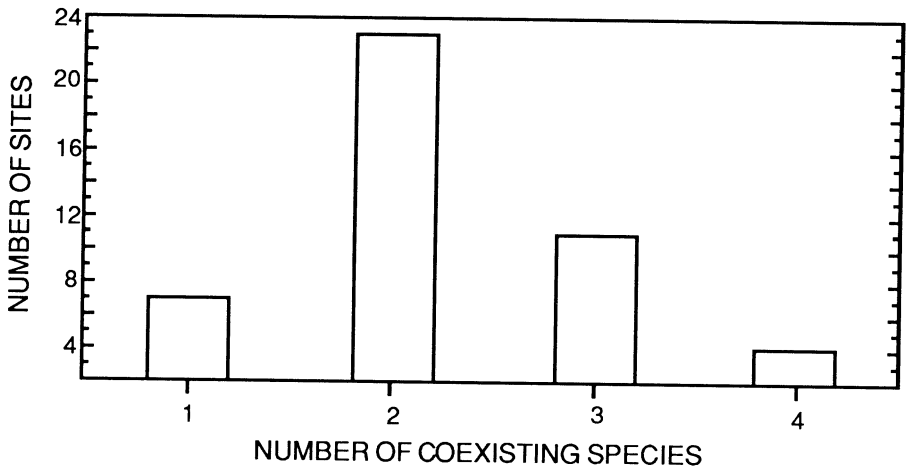


FIGURE 6. Number of *Cnemidophorus* species at sites.

Geographical ranges

Despite the wider range of macrohabitats occupied by parthenogenetic *Cnemidophorus* species, their geographical ranges are rather restricted compared with other lizards. Table 8 presents statistics for range size for a variety of lizard groupings. Unisexual whiptails have the smallest ranges of any group. Their ranges are significantly smaller than for bisexual forms (Mann-Whitney test; $P < .01$) as well as U.S. lizards in general (65 species, M-W test; $P < .02$). Most U.S. lizards with small ranges are restricted to one or two ecological associations; for example, the specialist fringe-toed lizards, *Uma*, in California (Stebbins, 1966). The all-female whiptails, however, have broad habitat ranges, but small geographic distributions.

Comparison with other studies

The average time niche overlap for 37 North American diurnal lizard species pairs studied by Pianka (1973) was 0.86. Thus, these whiptails overlap somewhat more than the "average" lizard species pair (mean time overlap for whiptails is 0.92). Whiptails are active at similar times, even more similar than if time niches were random (Pianka, *et al.* [1976] find that if North American lizards used times randomly, overlaps should be about 0.52). Microhabitat overlap for 55 pairs of North American lizard species averages 0.46 (Pianka, 1986). The Trans-Pecos *Cnemidophorus* overlap in microhabitats by an average of 0.82. Last, dietary overlap aver-

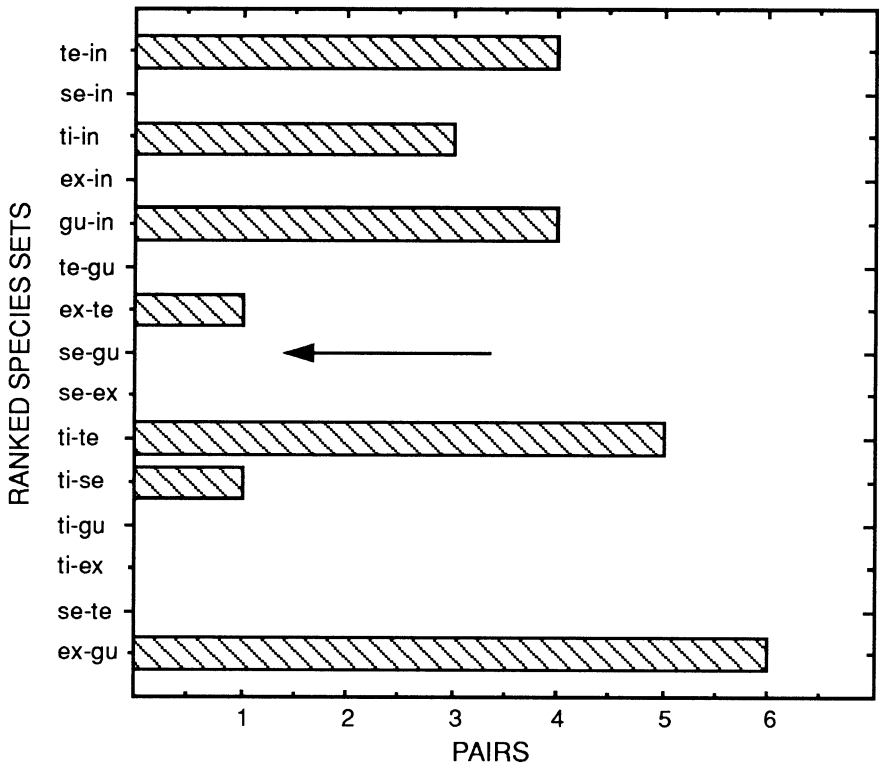


FIGURE 7. Possible pairs of species of *Cnemidophorus* studied in Trans-Pecos Texas. First two letters of specific name given. Number of sites given as "Pairs." Pairs are ordered from those with greatest difference in body size (top) to least difference (bottom) as given in Case (1983). Arrow indicates mode. See text for details.

aged 0.31 in North America (Pianka, 1986) and 0.82 for the *Cnemidophorus* studied here.

Discussion

The Wright and Lowe hypothesis (1968) proposed that parthenogenetic *Cnemidophorus* are of hybrid origin which would explain their very high levels of heterozygosity. This part of the hypothesis has been confirmed by a long series of studies (for example, Densmore *et al.*, 1989; Moritz *et al.*, 1992). The hypothesis then states that the hybrid, highly heterozygous nature of the all-female whiptails allows them to exploit ecotonal zones. Wright and Lowe provide convincing evidence that the

TABLE 7. Geographic ranges for various lizard groups in the United States. Range is in number of 1° latitude X 1° longitude squares included in the species' ranges. Mean and SD followed by number of species used in the calculation.

Species Group	Mean Range	SD	N
Unisexual <i>Cnemidophorus</i>	29.6	10.3	5
Bisexual <i>Cnemidophorus</i>	159.2	138.71	4
<i>Sceloporus</i>	110.6	125.4	10
<i>Phrynosoma</i>	69.3	58.8	7
Other Iguania	68.7	60.7	17
Skinks	141.4	90.7	11
Other lizards	44.1	59.1	16
All <i>Cnemidophorus</i>	87.2	109.3	9
All Iguania	81.2	84.1	34
All non <i>Cnemidophorus</i>	82.3	84.6	61
All lizards	82.9	87.3	70

unisexual species are found over geographic regions that have been most severely altered by changing climatic patterns. Also, the small geographic ranges of the all-female species suggests they are of fairly recent origin and have not expanded much beyond the ecotonal zones described by Wright and Lowe. Last, if the "weed" analogy is continued to its logical conclusion, we would expect the all-female species to be ecological generalists, overlap greatly with other whiptails in resources used, and be poor competitors restricted to disturbed zones where an equilibrium has not yet been established. Thus the weed hypothesis would explain how so many species of *Cnemidophorus* can coexist in the Trans-Pecos. How well is this last extension of the weed hypothesis supported by the data?

No obvious resource partitioning was detected in previous studies on the Trans-Pecos *Cnemidophorus* system, nothing to suggest that the whiptails follow the same sort of "assembly rules" proposed for other complex congeneric assemblages of lizards. The weed hypothesis suggests the bisexual species may well follow assembly rules based on resource partitioning, but the all-female species are fugitives that use precompetitive habitats. Assembly rules have been proposed for many assemblages of species (mostly vertebrates), but this practice has been strongly criticized (see Strong *et al.* [1984] for an introduction to this controversy). Critics argue that random association of species from a geographically-determined species pool will produce assemblages very similar to those that are actually seen. Thus, the "patterns" seen in these cases, and assembly rules proposed, are actually a spurious result of *post hoc* story-telling. In reply,

Pianka (1986) and Case (1983) present rigorous ways to determine if species are randomly associated, and give convincing data and analysis that at least some lizard communities are organized by interspecific interactions. For the weed hypothesis to avoid a charge of *post hoc* pleading for a special case, it should suggest logical predictions based on a knowledge of *Cnemidophorus* biology. Each aspect of the biology of the whiptails studied in this project will now be examined to determine compliance with the weed hypothesis.

The *Cnemidophorus* species in southwestern Texas present a guild of widely foraging, rapidly moving insectivorous lizards. The widely foraging tactic of whiptail lizards seems uniform throughout the genus, even for species that are primarily herbivorous (Dearing and Schall, 1992). Foraging in this way must influence other aspects of whiptail ecology, such as reproduction and thermoregulation (Schall, 1977, 1978, 1981; Dearing and Schall, 1993). What kind of differences might be expected among species if they do, in fact, partition resources?

As most energy expended in prey acquisition by a widely foraging lizard is consumed in the search, every palatable prey item below a minimum size should be attacked and consumed. This idea was confirmed by the data on prey taxa eaten by the whiptails -- overlaps in diet were very high. The whiptails ate mostly termites, a concentrated, nutritious food source which is not exploited by other lizards (and perhaps not by many other predators as well). Maximum prey size should differ only for lizards with very different body size, exactly as seen here. *C. inornatus*, the only really small species, takes significantly smaller largest prey. Larger species will eat the same prey sizes consumed by the smallest species, but once a bulky prey item is consumed by a large lizard it may be satiated and cease foraging, reducing competition with *C. inornatus*. Moreover, the most common prey type, the small termites, probably have a very rapid recruitment rate. I conclude that the data provide no evidence for a difference between the all-female and bisexual species in patterns in diet, but the smallest species may well use a different size range of prey items.

Times of activity were similar for all five species. Presumed preferred body temperatures are also similar for all species; that is, the all-female species do not have a broader thermal tolerance and preference compared to the bisexual species (Schall, 1977). Most likely, optimal body temperature is a conservative trait in these lizards and not likely to change even under the impact of hybridization. Foraging time, as opposed to duration of above-ground time when the lizards are out of their burrows, may be short during the hot desert summer, so all species may need to make full use of this relatively short period. Thus, time when active is not likely to differ among species.

Thus, habitat, both at the fine and coarse scale, is the niche dimension most likely to differ among widely foraging species such as *Cnemidophorus*, and this is what was originally discussed by Wright and Lowe when they proposed the weed hypothesis. The data show that *C. tigris* and *C. gularis*, the two larger bisexual species, use different habitat types. However, this preference is not fixed for the species. I have seen *C. gularis* in creosote flat desert habitat east of my study region, beyond the range of *C. tigris*. In the El Paso area (site 29), *C. tigris* occurs alone in a patch of grassy habitat outside the range of *C. gularis*. Both of these species can live in habitat that they appear to avoid where they are sympatric.

The two all-female species can be found with any of the other whiptails and in all kinds of habitat. Zweifel long ago (1965) noted the "...unpredictable choice of habitat of (*C. tessellatus*)," and this is what was observed here. *C. tessellatus* and *C. exsanguis* had the broadest microhabitat niche breadths of the five species, approximately 25% broader than the three bisexual species. The all-female species are found in a much broader range of macrohabitat types compared to the two larger bisexual species. They are, however, most common in disturbed zones. Indeed, the range maps for *C. tessellatus* and *C. exsanguis* should look like a net, with strands following roads, frequently disturbed draws, and even towns. Species association data in contrast suggest that the all-female species tend to be in habitats preferred by one of their bisexual ancestor species. Also, patterns of overlap in microhabitats do not differ between the parthenogenetic and bisexual species. I conclude that data on microhabitats only weakly support the weed hypothesis, but the general kind of habitats chosen by *C. exsanguis* and *C. tessellatus* are broader and tend to be disturbed zones where population sizes of lizards may not have reached their carrying capacities.

If only the bisexual species of *Cnemidophorus* existed in the Trans-Pecos, they could be used as yet another example of typical resource partitioning by congeneric lizards: two larger species with mutually exclusive habitat use and a small species that takes smaller prey. When the all-female species are included, the data provide weak support for the weed hypothesis as an explanation of the forces that shape the whiptail assemblage in southwestern Texas. Milstead followed up on his original study several years later (1965) and found dramatic changes in species composition at his study areas. This argues that the final resolution of the issues raised here will require long-term studies of turn-over of species at sites viewed as stable and those that are frequently disturbed. If the all-female species are fugitive or weedy species, the "cyclic sympatry" suggested by Scudday (1971) should occur at disturbed sites when the parthenogenetic species take advantage of habitat where lizard densities have been greatly reduced.

Pianka's recent (1992) study of the effect of disturbance on lizard community structure in the Australian desert illustrates the importance of such long-term studies. In the Trans-Pecos, the paradox of the whiptails still invites resolution.

Acknowledgments

For vital help in the field I thank R. W. Schall who spotted far more than half of the lizards we collected. Other field helpers included E. R. Pianka, G. Pool, and P. Levin. Landowners too numerous to mention allowed me access to their properties, but special thanks go to D. J. Sibley, K. G. Thompson, G. Mills, and the National Park Service. Critical suggestions and ideas came from E. R. Pianka, J. Wright, G. Pool, L. Lawlor, C. J. Cole, T. Uzzell, W. Cade, L. Gilbert, D. Feener, L. Lundelius, A. Templeton, and J. A. Joern. The work was funded by grants from the American Museum of Natural History, the Society of the Sigma Xi, and the National Science Foundation.

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