

## Phenology of a Lizard Assemblage in the Dry Chaco of Argentina

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**ABSTRACT.**—Individual species' phenologies can play an important role in the structure of lizard assemblages over short time scales. Data from a pitfall study carried out in the dry Chaco of Argentina were used to address the question of how species are distributed in their assemblage through time. Lizard activity and species richness were highest in the spring breeding season and declined in the cool months of the year. Variations in seasonal activity patterns and reproductive chronology resulted in significantly different distributions of species in every sample month. Not only did the species composition of the assemblage change through time, but the mean size of lizards and the proportions of males, females, and juveniles varied significantly for several species. Large lizards, regardless of species, disappeared from the assemblage during the cool, dry winter, while juveniles of the large species remained active year round. Adults of the smallest species were also active throughout the year. We propose an hypothesis based on thermoregulatory constraints of lizard body size to account for these patterns. An approach focusing on the energetics and physiological ecology of individual species would be fruitful in understanding the dynamics of fluctuating lizard communities.

Most studies of lizard communities have addressed how species partition food resources and habitat (Barbault and Maury, 1981; Creusere and Whitford, 1982; Heatwole, 1982; Pianka, 1973, 1986; Vitt and Zani, 1996). We have learned from these studies that over evolutionary time, lizard communities appear to be structured mainly by processes that resulted in niche segregation primarily through microhabitat use, diet, or daily activity regimes (Pianka, 1994; Vitt, 1995).

This study differs in that we are not asking how lizard assemblages are structured in terms of their patterns of resource use, but rather how species are distributed in their assemblage over time. As seasons change from warm to cool and wet to dry, characteristics of species assemblages may also change. Individual species' phenologies are consequences of factors such as the timing of reproduction, seasonal activity patterns, and population dynamics. We suggest differences among species' phenologies can play an important role in the composition of an assemblage over relatively short time scales. Barbault (1991) pointed out the structure and dynamics of tropical lizard communities may depend largely on differences in species' ecologies. Using three sympatric skinks as an example, he argued that habitat preferences and timing of reproduction were largely responsible for observed patterns of temporal community structure. Variation in timing of reproduction among species may influence the dynamics of lizard assemblages through temporal fluctuations in the

structure of populations, and consequently in the absolute and relative abundances of species. Hence, because of fluctuations in population sizes and structures associated with the recruitment of small (neonate) lizards into the assemblage, we may expect important temporal variation to exist in the sizes of lizards operating in the environment over short time periods. Seasonal activity patterns are also predicted to vary among species. Entire species may be inactive during winter, for example, while others may be represented only by juveniles. Hence, different suites of species, and life stages of individual species, may be dominant in the environment at different times due to abiotic constraints.

If such patterns do occur, important temporal variation should exist in the numbers, kinds, and sizes of lizards active in the environment over short time periods. The presence of differing suites of lizards active at different times could influence the role of lizards as predators, prey, and competitors in the ecosystem. It is interesting to ask whether profound temporal changes in community dynamics exist, and if they do, are they the consequence of species' phenologies? If species specific phenologies account for temporal variation in structure of an assemblage, what factors best explain the differences?

To gain insight into these questions, we describe the annual cycle of changes in species composition, species number, and population structure for an assemblage of lizards in the dry Chaco of Argentina and elucidate the impor-

tance of variation in the yearly cycles to short-term dynamics of the lizard assemblage. Species lists have previously been compiled for Chaco herpetofauna (Scott and Lovett, 1975; Gallardo, 1979; Cei, 1993; Cruz et al., 1993), but this is the first study to document the composition of a lizard fauna in the Chaco. We interpret the resulting patterns of temporal dynamics for this assemblage, and evaluate alternative hypotheses based on energetics and thermoregulatory constraints of lizard body size that explain the observed patterns.

#### MATERIALS AND METHODS

*Study Area.*—The study site was a 10,000 ha forest near the town of Joaquin V. Gonzalez, Salta, Argentina (25° S, 64° W). This region of semi-arid biome of the Argentine Chaco is characterized by a hot rainy summer and a cool dry winter. The hottest temperatures in South America, over 46°, have been registered in this region, while temperatures in May through September may fall below freezing (Bucher, 1974). The dry chaco is characterized by distinct rainy and dry seasons, with rains typically beginning in November and continuing through the warm months until March. Very little rain falls between May and September. The average annual rainfall during the 54 yr period between 1935 and 1988 was 553 mm (Fitzgerald et al., 1993). Rainfall is variable, and extremes in annual rainfall occurred during the two years of this study; 1987 was the wettest year in the preceding 54 with 957 mm of precipitation, while 1988 was a drought year with only 290 mm of rain.

Vegetation at the study site was a dense, botanically complex, thorn forest (Bucher, 1982). Emergent trees were predominantly red and white quebracho (*Schinopsis quebracho-colorado* and *Aspidosperma quebracho-blanco*), and the forest on average was 10–15 m tall. Most of this forest was cleared in the 1990s.

Lizards were sampled from December 1987 to May 1988 and from October 1988 through October 1989 with a combination of seven trapping arrays and a linear transect of 46 pitfall traps spaced every 50 m along alternate sides of a dirt track through the forest. Each trapping array consisted of four, 8-m long drift fences with pitfall traps on each end, arranged in an open cross design (Campbell and Christman, 1982). Fifty-six pitfalls were used in the seven arrays. Pitfalls were fashioned from galvanized flashing with a concrete bottom and wooden cover, 34 cm in diameter × 72 cm deep. Each trap array was separated by >800 m from other arrays and the transect to minimize effects of removing individuals from the lizard populations, to minimize spatial autocorrelation among trap sites, and to ensure adequate coverage of microhabi-

tat in the study area. Each trap array and single trap along the transect thus represented very small sinks in comparatively large source areas.

Traps were checked sporadically each month, depending on accessibility and flooding at this remote site. Because of reduced lizard activity in the cold season, we checked the traps once each month from April through September. Lizards taken from the traps were preserved, and later their snout-vent lengths (SVL) were measured and sex determined. All specimens are deposited in the research collections of Instituto de Herpetología, Fundación Miguel Lillo, Tucumán, Argentina.

*Analyses.*—Biases result from differential trapabilities of species (Campbell and Christman, 1982; Bury and Corn, 1987), thus we did not treat the data as indicators of absolute population density. Occurrence of lizards in the traps resulted from a combination of population density, activity level, and distance individuals move when active (James, 1994). Our approach has been to evaluate shifting patterns of species composition through time by comparing the relative numbers of individuals of each species. Hence, we assumed that trapping data provided reliable information on changes in the abundances and activity of each species over time (James, 1994). Lizard captures were standardized according to trapping effort (i.e., lizards/trap). To analyze for differences in composition of the assemblage, significantly different distributions of species among months or years were identified with Friedman 2-way ANOVA and contingency analysis. We contrasted the frequency of occurrence of each species to the pooled frequencies of the other five species during 13 consecutive trapping months using contingency tables (Zar, 1996). We formulated the null hypothesis,  $H_0$ : the distribution of each species across sample months is no different from that of the rest of the assemblage pooled. A Bonferroni correction was applied to the  $P$ -values resulting from the contrasts. Expected frequencies were small in a few cells, but all tables had 12 degrees of freedom and were thus extremely robust to Type I errors. Lewontin and Felsenstein (1965) showed that when degrees of freedom is >5, homogeneity tests are conservative at the 0.01 level of significance if expected frequencies are <1. Contingency analyses were useful for examining the relative importance of each taxon in the assemblage through time. Deviations of the actual occurrence of each species from its expected frequency were scaled from -1 to 1 to illustrate relative changes in the occurrence of each species. Analysis of Variance and Dunnett's post-hoc comparisons for unequal variances were used to compare species' mean SVLs among months; months with only

TABLE 1. Occurrence of lizard species in the vicinity of Joaquin V. Gonzalez, Salta, Argentina during the study period.

Family Species	Number in traps (percent of total trapped)
<b>Gekkonidae (2 species)</b>	
<i>Homonota fasciata</i>	97 (10.6%)
<i>H. borelli</i>	2 (0.2%)
<b>Tropiduridae (6 species)</b>	
<i>Liolaemus chacoensis</i>	131 (14.3%)
<i>L. weigmanni</i>	12 (1.3%)
<i>Stenocercus doellojuradoi</i>	6 (0.7%)
<i>Tropidurus etheridgei</i>	255 (27.7%)
<i>T. spinulosus</i>	1 (0.1%)
<b>Polychrotidae (1 species)</b>	
<i>Urostrophus gallardoi</i>	4 (0.4%)
<b>Teiidae (5 species)</b>	
<i>Teius teyou</i>	143 (15.6%)
<i>Cnemidophorus ocellifer</i>	171 (18.6%)
<i>Tupinambis rufescens</i>	17 (1.8%)
<i>Ameiva ameiva</i>	captured by hand
<i>Kentropyx viridistriga</i>	captured by hand
<b>Gymnophthalmidae (2 species)</b>	
<i>Vanzosaura rubricauda</i>	74 (8.1%)
<i>Pantodactylus schreibersi</i>	1 (0.1%)
<b>Scincidae (1 species)</b>	
<i>Mabuya frenata</i>	5 (0.5%)
<b>Anguidae (1 species)</b>	
<i>Ophiodon intermedia</i>	captured by hand

one individual were not included in the analyses.

## RESULTS

Of the 17 lizard species that occurred in the vicinity of the study site (Cruz et al., 1993), 14 were captured in traps. The families Teiidae, Tropiduridae, and Gymnophthalmidae accounted for 88.2% of the 919 pitfall and array captures, and Gekkonidae another 10.8% (Table 1).

The six most numerous species in the traps (Table 2) made up 94.8% of all captures during the study. Subsequent analyses were restricted to these six species as the assemblage of interest. These species are all insectivorous (Ceï, 1986, 1993), though the relatively large *Teius teyou* (Daudin) also eats some fruit (pers. observ.). Species differed in size (Table 2) and foraging habits. The tropidurids, *Tropidurus etheridgei* and *Liolaemus chacoensis*, were sit-and-wait foragers, while the teiids *Teius teyou* and *Cnemidophorus ocellifer* (Spix) were wide-ranging active foragers (Regal, 1983; Vitt, 1983). The Gymnophthalmid *Vanzosaura rubricauda* (Boulenger) and the nocturnal gekkonid *Homonota fasciata* (Duméril and Bibron) were denizens of the left litter.

**Temporal Patterns of Species Composition.**—Increased activity during spring was reflected in increased trapping success (Fig. 1). Forty-nine percent of all captures during the 1988–1989 season (October 1988 to September 1989) were made in October and November, and activity declined throughout the summer. In contrast, only 9.7% of the captures in 1988–1989 occurred during the winter months, June through August combined. Species richness peaked during spring and varied between seven and nine during summer in both sampling periods. Species richness dropped to between three and seven species during fall and winter (Fig. 1).

The total number of lizards captured from December through May was similar between years (176 captures in 1987–1988 compared to 190 captures in 1988–1989), but contingency analysis revealed significant differences in the numbers of each species captured between years. ( $\chi^2 = 21.1$ ,  $DF = 5$ ,  $P = 0.0008$ ) (Fig. 2). Fewer *V. rubricauda* were trapped than expected in 1988–1989 and more *L. chacoensis* and *H. fasciata* were trapped than expected in 1988–1989.

Significant patterns in the association of species across 13 consecutive months (Oct 1988–Oct 1989) were clearly revealed (Friedman test statistic corrected for ties = 40.2,  $df = 5$ ,  $P <$

TABLE 2. Mean SVL  $\pm$  one standard deviation (mm) for males, females, and juveniles of six species used in analyses of community composition. The values in bold typeface denote groups or species that were active throughout 1988–89. *Teius teyou* and the adults of *Cnemidophorus ocellifer* and *Tropidurus etheridgei* were inactive during cool months.

Species	Male	Female	Juvenile
	$\bar{x}$ SVL $\pm$ SD (n)	$\bar{x}$ SVL $\pm$ SD (n)	$\bar{x}$ SVL $\pm$ SD (n)
<i>Teius teyou</i>	105.56 $\pm$ 20.86 (72)	99.03 $\pm$ 18.70 (54)	51.65 $\pm$ 7.24 (13)
<i>Cnemidophorus ocellifer</i>	59.72 $\pm$ 4.77 (94)	57.83 $\pm$ 6.21 (54)	41.07 $\pm$ 6.65 (23)
<i>Vanzosaura rubricauda</i>	<b>32.77 <math>\pm</math> 2.17 (42)</b>	<b>37.20 <math>\pm</math> 2.81 (26)</b>	<b>24.53 <math>\pm</math> 3.01 (3)</b>
<i>Tropidurus etheridgei</i>	71.37 $\pm$ 11.16 (96)	66.10 $\pm$ 7.78 (86)	37.78 $\pm$ 6.68 (73)
<i>Liolaemus chacoensis</i>	<b>38.91 <math>\pm</math> 3.74 (75)</b>	<b>41.13 <math>\pm</math> 5.75 (40)</b>	25.35 $\pm$ 5.77 (16)
<i>Homonota fasciata</i>	49.05 $\pm$ 5.01 (64)	48.97 $\pm$ 6.64 (15)	28.34 $\pm$ 4.61 (18)

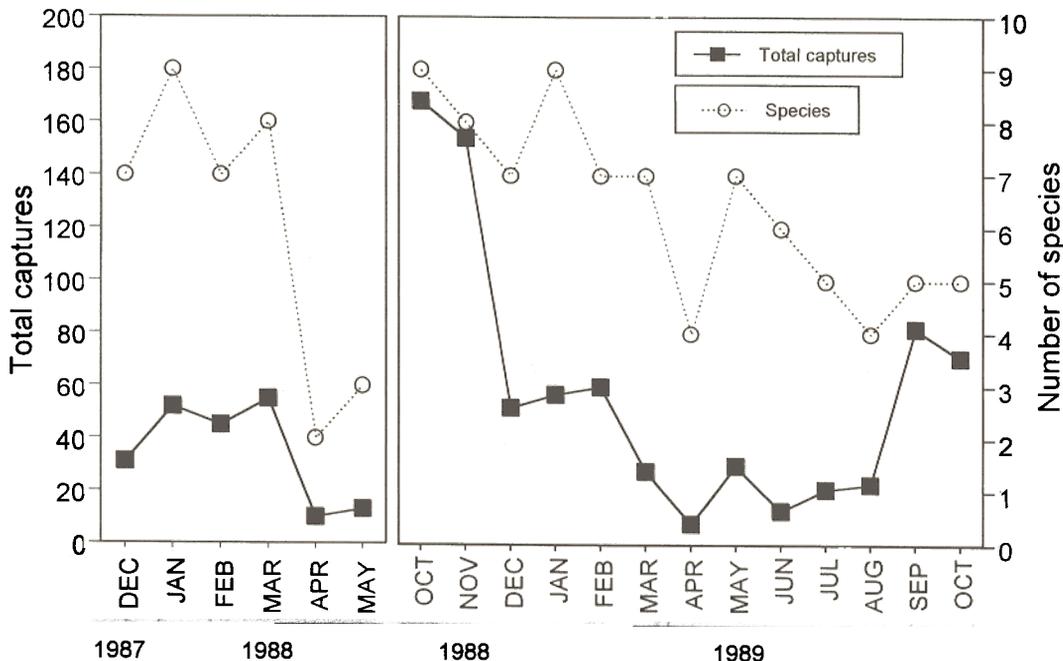


FIG. 1. The total number of captures of lizards and the number of lizard species in each monthly sample.

0.0001). Interestingly, each species was uniquely distributed compared to the distribution of the other members of the assemblage. Contrasts revealed statistically significant differences in the phenologies of each species relative to the others. Graphs of deviations from expected frequencies standardized to a scale of  $-1.0$  to  $1.0$  demonstrated months when each species occurred more or less frequently than expected ( $P < 0.005$  for all contrasts, Fig. 3).

*Teius teyou*, the largest member of the six-taxon assemblage, showed a cyclic pattern in which the highest capture rates were associated with the hottest months. *Teius teyou* was represented in the traps much more than expected from November through January, but disappeared completely after March. The remaining species remained active to some extent year round (Fig. 2). *Cnemidophorus ocellifer*, another teiid, was collected in every month except June. *Cnemidophorus ocellifer* was under-represented in October and November in 1988, but was abundant in September and October 1989. *Tropidurus etheridgei* and *L. chacoensis*, occurred together in all months except April and May 1988 and May 1989. *Liolaemus chacoensis* was trapped more than any other species in July, August, and September. *Tropidurus etheridgei*, was the only species trapped every month, and was the most numerous species in 11 of 19 trapping months. *Tropidurus etheridgei* occurred in relatively high abundance during spring, and hatchling *T. eth-*

*eridgei* dominated the assemblage during the cool dry months. *Vanzosaura rubricauda* occurred in consistently low numbers throughout the year except for the breeding season months of October through December, when 64.9% of all individuals of that species were collected. *Homonota fasciata* was trapped more than expected in spring of 1988 but less in spring 1989 (Fig. 3).

**Population Structure and Body Size.**—As the lizard assemblage varied in species composition, so did the structure and average sizes of the lizard populations. The proportions of sexes and juveniles for *T. teyou*, *C. ocellifer*, and *T. etheridgei* were distributed significantly differently among months (Fig. 3; Total  $\chi^2 = 29.2$ ,  $P < 0.001$ ; Total  $\chi^2 = 47.7$ ,  $P < 0.001$ ; Total  $\chi^2 = 170.6$ ,  $P < 0.001$ , respectively). More male *T. teyou* and *C. ocellifer* were collected in October and November than expected, while the proportions of juveniles of these species increased in February through May, corresponding to the appearance of hatchlings. The same pattern was apparently exhibited by *L. chacoensis* and *H. fasciata*, but sample sizes precluded statistical comparisons. The pattern for *T. etheridgei* was somewhat different. Sex ratio was relatively even during the spring and summer months, while practically the entire samples taken in March through August were made up of juveniles (Fig. 4).

Because of the appearance of hatchlings and the concomitant disappearance of adults of several species, the sizes of lizards that were active

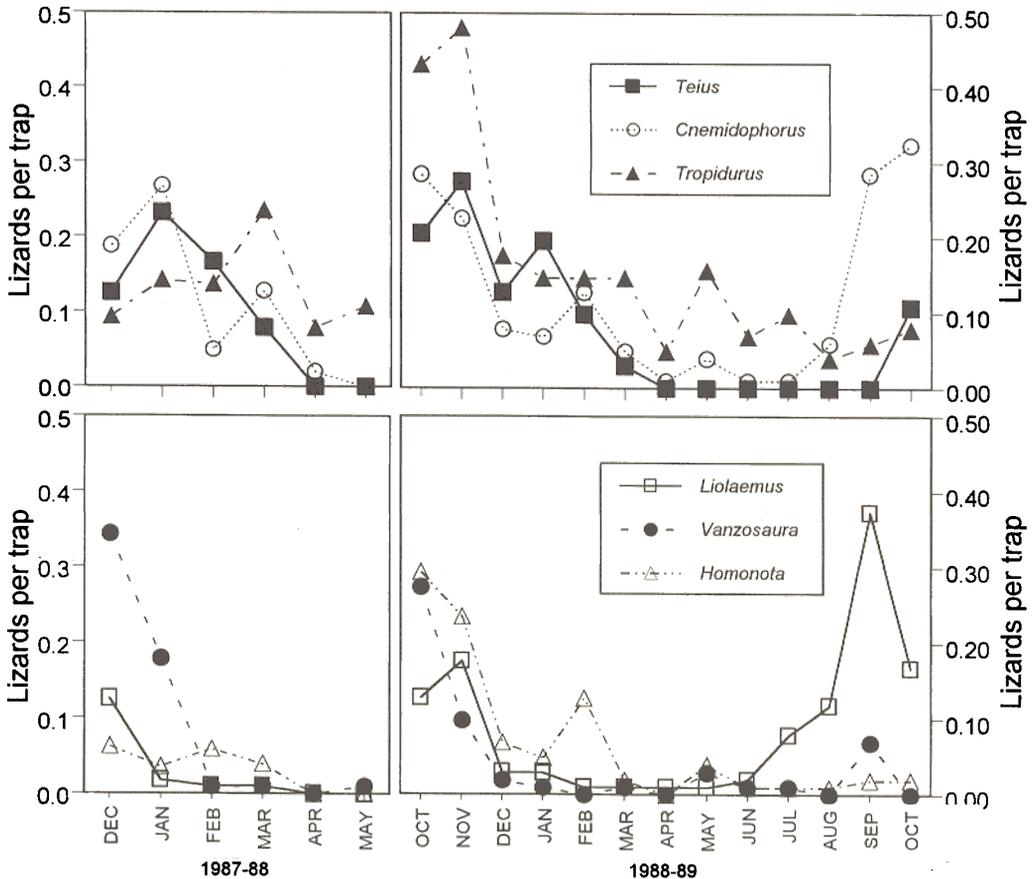


FIG. 2. Trends in the standardized number of each lizard species captured throughout the study.

varied at different times. The mean SVLs were significantly smaller in March for *L. chacoensis* and *T. teyou*, and in March, April, and May for *T. etheridgei* ( $F_{9,129} = 9.55$ ,  $P < 0.001$ ;  $F_{5,138} = 5.14$ ,  $P < 0.001$ ;  $F_{10,253} = 22.74$ ,  $P < 0.001$ , respectively). Similarly, mean SVLs of *V. rubricauda*, *C. ocellifer*, and *H. fasciata* varied significantly among sample months ( $F_{7,69} = 2.69$ ,  $P < 0.02$ ;  $F_{8,168} = 4.36$ ,  $P < 0.001$ ;  $F_{7,94} = 3.39$ ,  $P < 0.003$ ), but a posteriori comparisons did not discriminate groups of means. The mean SVLs for these species were slightly smaller during the cool months (Fig. 5).

#### DISCUSSION

Our results converged on the conclusion that differences in activity patterns and reproductive cycles of different species played an important role in the temporal structure of lizard assemblages in the fluctuating Chaco environment. These differences resulted in distinct assemblages in every sample month. During the spring months, more species were present and the activity level of the entire assemblage was

at its peak, while overall activity was reduced in the fall and winter and fewer species were present.

The greater number of captures in September to November undoubtedly reflects generally high lizard activity associated with the spring mating period (Stamps, 1983). The general chronology of lizard reproduction in the Chaco is one where mating occurs in October and November, and hatchlings appear in February and March. The relatively high numbers of male *T. teyou* and *C. ocellifer* collected in October and November, for example, presumably corresponds to the characteristic pattern of increased activity exhibited by male teiids during the courting season (Regal, 1983). Reproductive characteristics, morphology, daily activity patterns, and diet are similar in teiids (Vitt and de Carvalho, 1995), hence it is not surprising the teiids in this assemblage exhibited similar phenologies (Anderson and Vitt, 1990). Studies of reproductive cycles of lizards at this site showed that *T. teyou*, *C. ocellifer*, and *Tupinambis rufescens* emerged from their burrows in spring with en-

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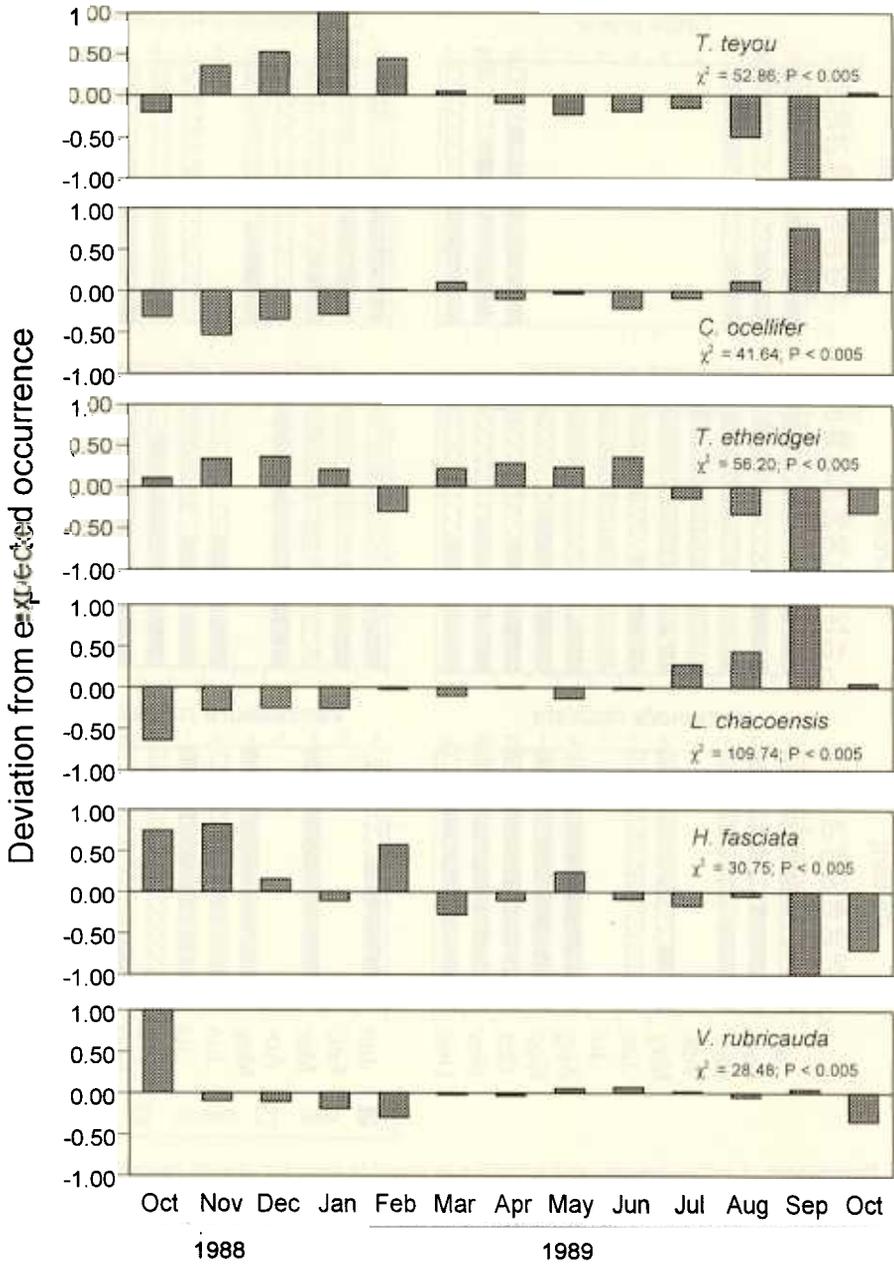


FIG. 3. Deviations from expected occurrence for each species in the lizard assemblage. The number of each species was contrasted to the pooled numbers of the other five species to test the null hypothesis that the distribution of each species across sample months did not differ from the rest of the assemblage. Deviations from expected frequencies were scaled from -1 to 1.

larged testes and ovarian follicles (Fitzgerald et al., 1993; Cruz, 1996a, b; Cruz et al., 1999). Concordant with reproduction, activity in *T. rufescens* was greater in spring than in other months, especially in large males that embarked on long foraging and mate-seeking excursions (Fitzgerald et al., 1991, pers. observ.). Similarly, based

on its abundance in December and October 1988, it is tempting to infer that *V. rubricauda* must roam over small ranges in the litter or underground during most of the year and expand its range substantially when seeking mates in the spring. Indeed, female *V. rubricauda* contained oviductal eggs in October (Cruz, 1994a).

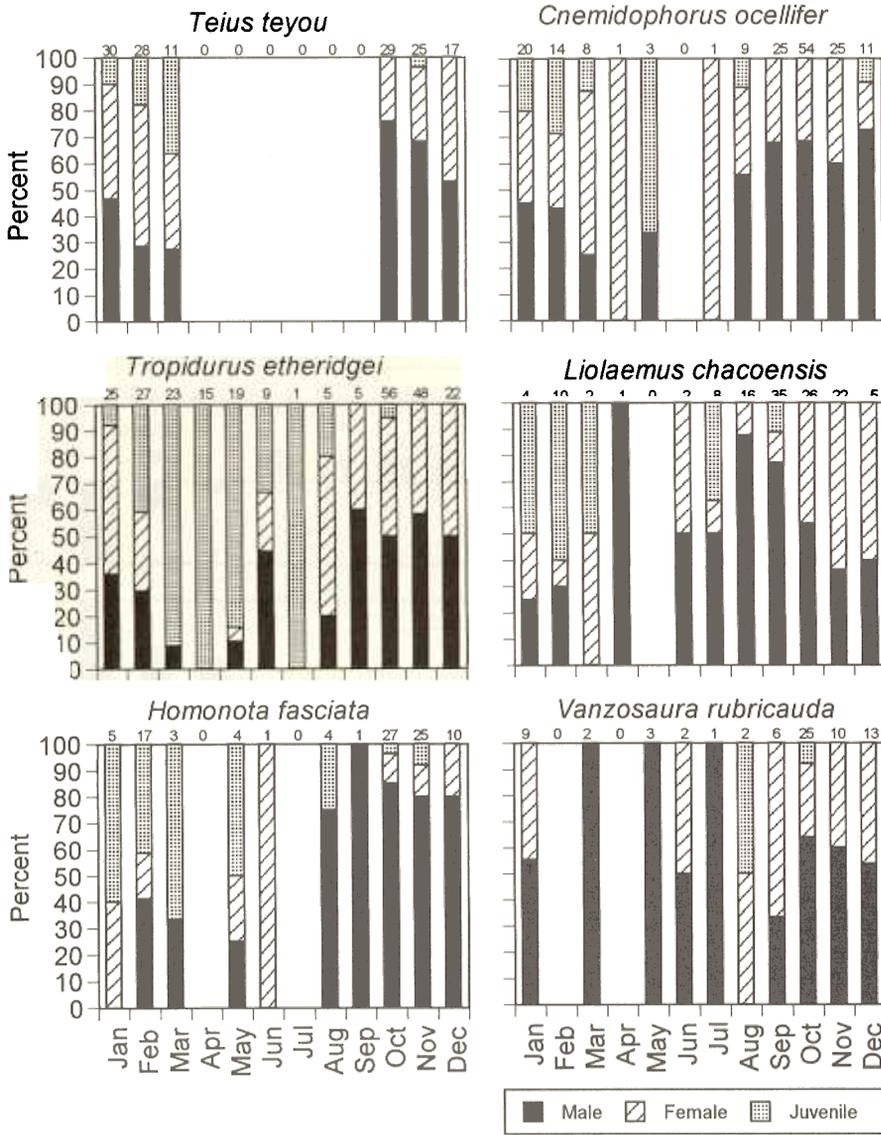


FIG. 4. Percentages of males, females and juveniles in monthly samples of each species. Months when zero individuals were captured were not used in analyses of population structure.

The breeding season for *H. fasciata* at our study site peaked somewhat later and was more protracted; reproduction occurred July through February, and hatchlings appeared in November and December (Cruz, 1994b).

Differences in the composition of the assemblage between years were probably due more to vagaries of trapping and stochastic population fluctuations than to a change in the distribution of species in the assemblage. *Liolaemus* spp. were much more abundant in spring 1989 than during any other period, for example. It would be interesting to investigate year-to-year variation

in the structure of lizard assemblages in response to longer environmental cycles.

Our study was limited by the short-term nature of our data, but the trends nevertheless represent a consistent yearly cycle in the structure of the assemblage. The question remains whether the overall pattern of the lizard assemblage was due entirely to independent phenologies of individual species, or if the assemblage exhibited a group phenology that was at least partly influenced by species interactions. Insight into questions aimed at species interactions, for example, "Do certain species remain active in the

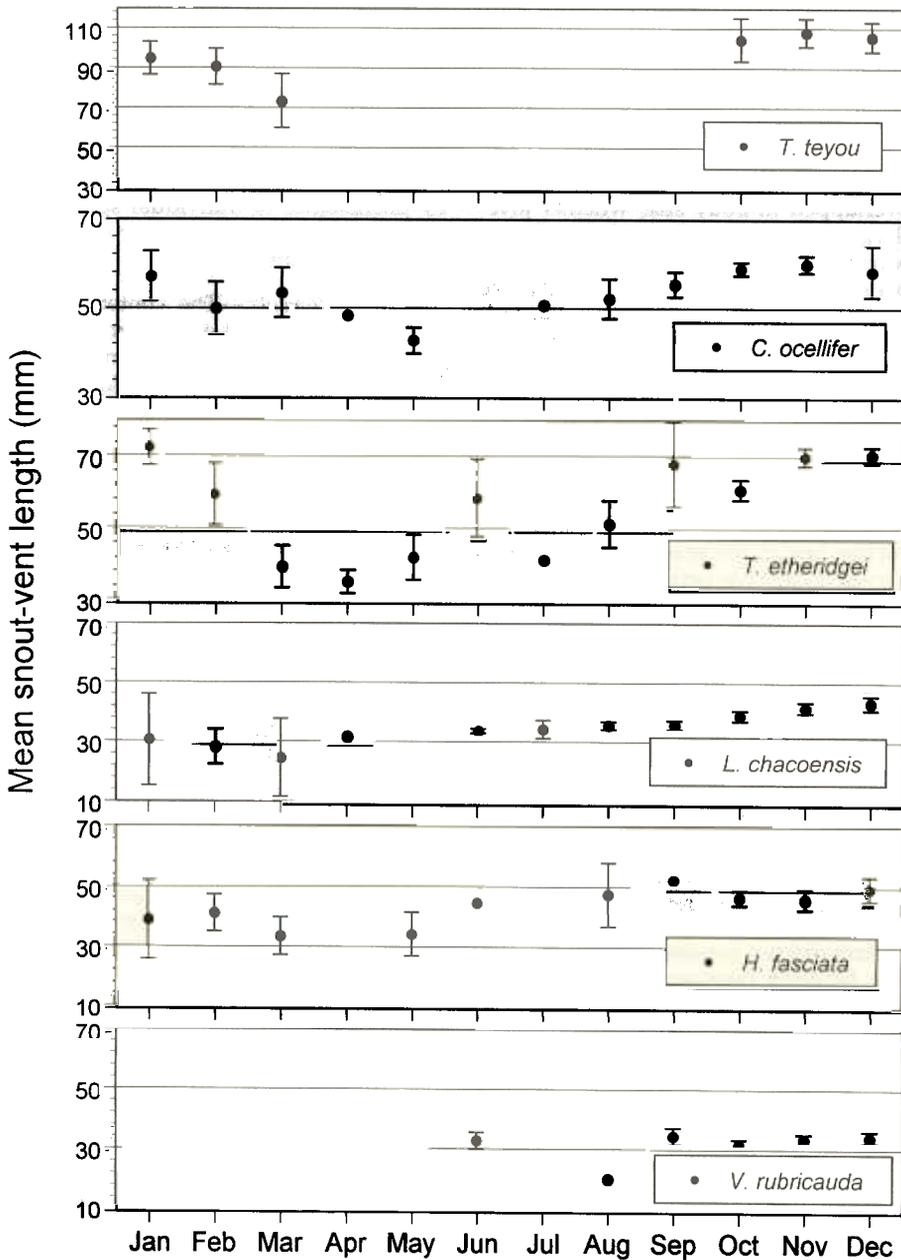


FIG. 5. Body size variation through time for each species in the lizard assemblage. Points are mean snout-vent lengths  $\pm$  2 standard errors (mm). ANOVA statistics are reported in the text.

absence of another species?", might be gained by comparing patterns of abundance and activity among assemblages composed of subsets of the same species. Experiments where species were removed from replicated plots would be an exciting and fruitful approach to understanding the role of species interactions in lizard assemblages.

An overriding pattern that emerged from the

analyses was the conspicuous absence of large lizards during the cool months, while juveniles of these species remained active. In March, almost all *T. teyou* captured were juveniles and this species dropped completely out of the assemblage by April. Only juveniles of *C. ocellifer*, *H. fasciata*, and *T. etheridgei* remained active in the cool, dry season. The same pattern has been documented for *T. rufescens* which, at up to 5

kg, was by far the largest lizard on the study site. *Tupinambis rufescens* appear in October at the site and disappear in March (Fitzgerald et al., 1991). Interestingly, both adults and juveniles of the smallest species, *Liolaemus* spp. and *V. rubricauda* were active year round. It is noteworthy that all the groups active during the winter overlapped in body size, whether juveniles of large species or adults and juveniles of small species (Table 2).

This pattern is compelling because body size influences almost everything lizards do, including the niche parameters proposed to drive community structure: habitat selection, diet, and activity (Pianka, 1986, 1994; Vitt, 1995). Several hypotheses can be formulated to explain the correlation between seasonal activity patterns and body size that we observed, but we favor two alternatives that are not necessarily exclusive. The first is based on energetics. Juveniles may be active late in the season to accumulate food reserves to survive periods of aestivation, to increase their growth during their juvenile period, or to have access to resources that were preempted by larger lizards while they were active. Interspecific interactions have been shown to play a role in structuring lizard communities (Schoener, 1974), and experimental manipulations have shown competition between lizards during periods of food scarcity (Dunham, 1980). For this scenario to be realistic, it must be costly for large lizards to remain active during the cool periods. For example, once an individual has accumulated enough energy reserves, it does not pay to remain active and be exposed to predators. Our data did not consistently support this hypothesis, however, because juveniles of *T. teyou* did not remain active, nor did juveniles of *T. rufescens*.

The second hypothesis depends on differential thermoregulatory constraints of lizards of different sizes. Large lizards may not remain active during cool months because they are unable to maintain sufficient body temperatures for long enough periods to maintain a cost effective energy budget. Because of the direct effects of body size on body temperature (Stevenson, 1985), differences in body size among lizards is strongly implicated in regulating lizard activity and habitat choice (Asplund, 1971). Hillman (1969) studied three sympatric *Ameiva* in Costa Rica and not only found differences in thermal habitats used by *Ameiva* of different species, but he also showed juveniles of the large species occupied the thermal habitat of the smaller species. This situation is consistent with our results, and in this regard supports the hypothesis. We feel that an approach focusing on the energetics and physiological ecology of individual species would be a fruitful avenue of research towards

understanding seasonal patterns in fluctuating communities. Until other studies demonstrate the likelihood that temporal patterns of lizard assemblages are explained by other processes, such as interactions among lizard species, we prefer to conclude the pattern exhibited by this assemblage could be explained almost entirely by phenologies of individual species, which in turn were determined by their life histories and abiotic constraints.

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