

LIZARD COMMUNITIES

Temporal and Spatial Resource Partitioning in a Chihuahuan Desert Lizard Community

by

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Abstract

Activity patterns of the lizards in a Chihuahuan Desert creosotebush (*Larrea tridentata*) community were studied by walking fixed transects on a marked grid and recording activity of individual lizards. We found considerable spatial overlap in *Cnemidophorus tigris* and *Holbrookia texana*; however, individuals that overlapped spatially were active at different times. We distinguished five distinct activity patterns in *C. tigris* and *H. texana*, whereas *Uta stansburiana*, *Sceloporus magister*, *Phrynosoma modestum*, *P. cornutum*, and *Crotaphytus wislizenii* were bimodal. Individual activity patterns varied: some were active only in the morning, only in midday, only in the afternoon, morning and afternoon, or all day. Most lizards were active less than 25 % of the days of observations. Exceptions were a few large male *H. texana* that were active between 40 % and 70 % of the days. We suggest that temporal separation of activity reduces intraspecific competition and increases carrying capacity in species for which food is probably not a limiting resource.

Recently there has been considerable interest in resource partitioning in lizard communities (Pianka 1973; Huey and Pianka 1977). Species typically divide resources along three dimensions: food type, habitat, and time (Pianka 1969); most studies have focused on habitat segregation, food size and body size, and daily and seasonal activity patterns (Schoener 1974). These studies, of necessity, have largely ignored differences in activity patterns among individuals in the populations of component species in order to focus on the overall patterns of resource partitioning. Several studies have shown that lizards in climatically varying habitats exhibit interspecific differences in activity periods (Inger 1959; Hillman 1969; Schoener 1970), but studies that have considered activity patterns of individuals have been limited to a single species (Irwin 1965; Simon and Middendorf 1976). Simon and Middendorf (1976) suggested that intraspecific partitioning may reduce competition, increase feeding efficiency, and increase carrying capacity. However, few studies have concentrated on temporal partitioning; Schoener (1974) indicated that temporal par-

titioning was much less important than food and habitat.

In studies of four sympatric species of Chihuahuan Desert ants, Whitford and Ettershank (1975) and Whitford (1978) showed that temporal partitioning was extremely important in species packing in Chihuahuan Desert ant communities; however, no attempt was made to follow the activity patterns of individual colonies.

Simon and Middendorf (1976) studied individual *Sceloporus jarrovi* and found that most adult activity was in the early morning and most juvenile activity occurred near noon. They also found that individual lizards were active an average of only 2.5 days per week.

In our studies of Chihuahuan Desert lizard communities (Whitford and Creusere 1977), we found seasonal differences in activity patterns of lizard species. We hypothesized that temporal partitioning might be as important in Chihuahuan Desert lizards as it seemed to be in the ants, and that there would be differences in activity patterns between juveniles and adults as suggested by Simon and Middendorf (1976). Therefore, we designed a study of the activity

patterns and microhabitat use of individual lizards of the eight species included in a Chihuahuan Desert lizard community. Here we report the results of that study.

Methods and Materials

The study area was on a watershed draining the southeast slopes of Mt. Summerford of the Doña Ana range on the New Mexico State University Ranch, 40 km NNE of Las Cruces, Doña Ana County, New Mexico. The watershed includes an alluvial fan (bajada) dissected by numerous ephemeral watercourses (arroyos) which drain into an ephemeral lake (playa). The soils on the bajada are shallow and sandy and the calcium carbonate deposition layer (caliche) occurs from a few centimeters to over a meter below the surface. The caliche layer is absent in arroyos that have complex soils varying from gravel to loam. The 50-year average precipitation for the area is 225 mm/year; peak rainfall occurs during July and August (Houghton 1972). Summer maximum air temperatures reach 40°C and freezing temperatures are recorded from October through mid-April (data from the Jornada Validation Site Weather Station).

The vegetation is typical of large areas in the northern Chihuahuan Desert. The well-drained areas on the bajada have an essentially monotypic cover of creosotebush, *Larrea tridentata* (23% cover), and all other species contribute about 1% cover. The arroyos are lined with a number of plant species including mesquite, *Prosopis glandulosa* (about 2% cover); tarbush, *Flourensia cernua* (1.5% cover); desert willow, *Chilopsis linearis* (< 1% cover); apache plume, *Fallugia paradoxa* (0.8% cover); and two yuccas, *Yucca elata* (0.2% cover) and *Y. baccata* (0.1% cover). The bajada slope varies from 5% to < 1%.

Studies were conducted on a 160- × 60-m grid bisected by a large arroyo. Nearly all lizards in this area were captured by pitfall traps, noosing, or hand-capture. Each individual was toe-clipped, marked by a tricolored code with enamel paint on its dorsum, and released. Marking had no visible effect on activity patterns and permitted positive field identification of a lizard without subsequent handling. The paint remained intact from 4 to 8 weeks and lizards

were repainted when identification became difficult.

A buffer grid was established 60 m on all sides of the main grid. The buffer was used to obtain complete home ranges of animals captured on the primary grid. No pitfall traps were established in the buffer zone. All species except *Cnemidophorus tigris* were either noosed or hand-captured and color-coded. Data for species activity was obtained from the main grid, whereas patterns of activity of individuals included data from both.

A predetermined transect across both grids was walked each hour to record individual activity throughout the day. When a lizard was observed, its color code, location, and time of observation were recorded. Data reported here are based on 100 15-h days of observation from May through October 1975. Climatic data for the periods of observation were obtained from a standard weather station on the site.

When a lizard is "active" on the surface, it spends time searching or waiting for prey alternating with or combined with thermoregulatory behavior. Data obtained from transects provided information only on the type of activity the individual was engaged in at that time. Therefore, we could not divide activity into component behaviors as is possible if individual lizards are followed for extended periods of time. In this study we define "activity" as any behavior occurring on the surface.

We could not use the method of Tanner and Krogh (1974) to evaluate activity. Their method assumes equal probability of sighting for all species. The Jornada is more densely vegetated than the Nevada Test Site studied by Tanner and Krogh (1974), particularly in the arroyos where large perennials block vision. Lizards were often heard but could not be identified before disappearing into shrubs or a burrow.

Behavioral characteristics of species had an effect on the reliability of the data. For example, some sightings of *C. tigris* could not be included in the analysis because the individual could not be identified. *Cnemidophorus tigris* was extremely wary and ran into a burrow if approached too closely. We were unable to approach this species to noose it, and had to rely on can traps for capture and painting. Even with binoculars it was difficult to identify individuals when they were running. There was also a high probability of missing cryptic species such as

Crotaphytus wislizenii and *Phrynosoma modestum*. *Holbrookia texana* was much less wary than *C. tigris* and could often be approached to within 10 m.

To compare species occurring at different densities, we weighted activity by setting the largest sum of all observations for an hour equal to 1.00 and expressing the activity in all other hours as a percentage of that sum.

Spatial overlap was determined by plotting the sightings of individual lizards on maps of the study area. Boundary lines were drawn connecting the outermost sightings for each individual, thereby enclosing the "area of activity." Area overlap between individuals of the same or different species was then taken from these plots. If all sightings of a given lizard were completely within the boundaries of the area of activity of another lizard, the spatial overlap was set at 1.00. Spatial overlap less than 1.00 was set as the percentage of activity area common to both lizards.

Results

Species Activity Patterns

Five species (*Crotaphytus wislizenii*, *Phrynosoma cornutum*, *P. modestum*, *Sceloporus magister*, and *Uta stansburiana*) had bimodal activity patterns. *Cnemidophorus tesselatus* had unimodal activity (in the morning only); *C. tigris* and *Holbrookia texana* were active most of the day (Fig. 1). *Cnemidophorus tesselatus* and *C. tigris* exhibited maximum activity between 0800 and 0900 h. *Sceloporus magister* had its maximum activity at 0730 h and *P. modestum* was most active at 1730 h. *Crotaphytus wislizenii* and *H. texana* exhibited peak activity between 1000 and 1100 h, and *Phrynosoma cornutum* was most active between 0730 and 0930 h. The afternoon peak activity was usually considerably shorter than the morning peak for all species; however, *U. stansburiana* was most active shortly after sunrise (0630 h) and between 1800 and 1900 h on days when cloud cover reduced insolation. Cloud cover appeared to depress the activity of all species except *U. stansburiana*. Nearly all individuals of this species were active on cloudy afternoons but were rarely encountered on clear afternoons. The most frequently observed lizard species were *H. tex-*

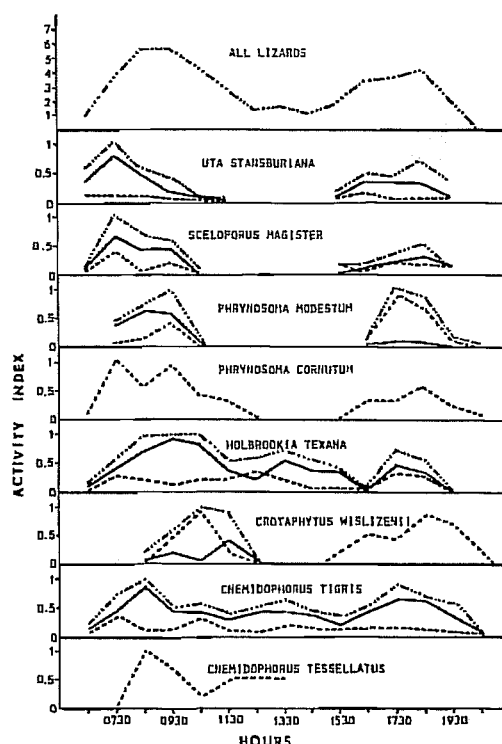


Fig. 1. Activity patterns of the lizards in a Chihuahuan Desert community. The activity index was derived by setting the largest number of observations equal to 1.00 and expressing the number of observations for all other hours as a fraction of 1.00. Dashed lines represent activity of females, solid lines the activity of males, and dot-dash lines the sum of the activity of all individuals seen, some of which were not sexed.

ana and *C. tigris*, which were also the most abundant (Whitford and Creusere 1977). We usually saw more males than females (Fig. 1).

Several hundred hours of observations yielded only 11 interspecific encounters. Seven of these resulted in both individuals fleeing a short distance, then immediately continuing their search for food. Three encounters between male *U. stansburiana* and *C. tigris* of both sexes resulted in the larger *C. tigris* ignoring the bobbing of the former and continuing its search for termites. The only successful interspecific defense of an area occurred when a female *P. cornutum* charged and pursued a large male *C. tigris* that had wandered into her territory while she was depositing eggs.

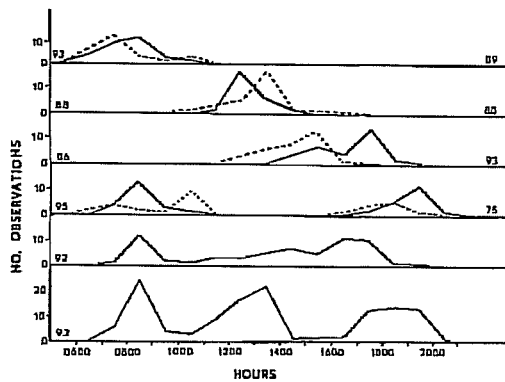


Fig. 2. Activity of the 10 most frequently encountered *Cnemidophorus tigris*. Dashed lines represent females, solid lines males. Snout-vent (S-V) lengths of males are on the left, S-V lengths of females on the right.

Individual Activity Patterns

Individuals in each species consistently maintained a preferred time of activity that made up only a portion of the total activity for the species. Within the populations of *C. tigris* and *H. texana*, we found five main patterns of daily activity: (1) early morning only, (2) midday only, (3) afternoon only, (4) both early morning and late afternoon, and (5) activity throughout most of the day (Figs. 2 and 3). The activity patterns of *U. stansburiana* are typical of species having a bimodal activity pattern. Individual lizards of bimodal species showed three patterns of activity: (1) morning only, (2) afternoons only, and (3) both morning and afternoon (Fig. 4). *Cnemidophorus tessellatus* was restricted to morning and midday activity on the study site but was observed to be active throughout the day in adjacent areas.

We made sufficient repeated observations on 30 of the 61 marked *C. tigris* to provide reliable estimates of individual activity patterns. Eight exhibited early morning activity, five were active only at midday, seven were active only in the afternoon, seven exhibited both morning and late afternoon activity, and three were active throughout most of the day. However, none of these individuals were seen on more than 25% of the days and most were seen only 10–15% of the days. The patterns of 10 of the most frequently encountered *C. tigris* are shown in Fig. 2. Of the 13 *H. texana*, 3 were active on-

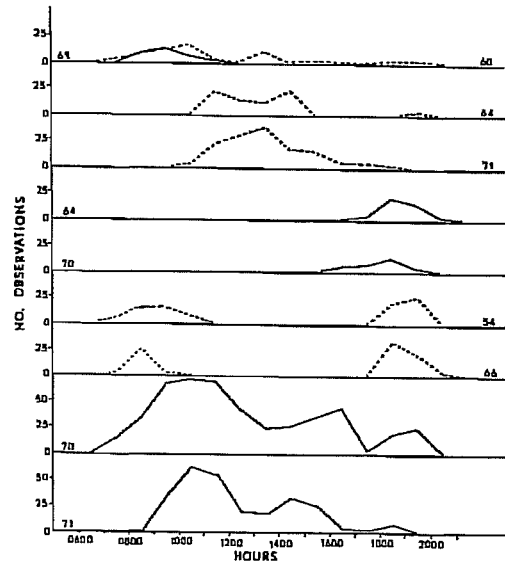


Fig. 3. Activity patterns of the 10 most frequently encountered *Holbrookia texana*. Dashed lines represent females, solid lines males. Snout-vent (S-V) lengths of males are on the left, S-V lengths of females on the right.

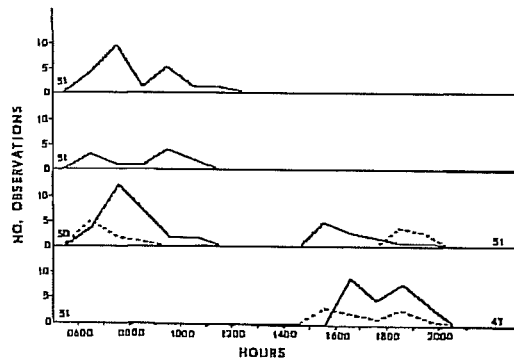


Fig. 4. Activity patterns of six *Uta stansburiana* selected to show the different activity patterns discussed in the text. Dashed lines represent females, solid lines males. Snout-vent (S-V) lengths of males are on the left, S-V lengths of females on the right.

ly in the mornings, 2 were active only in the afternoon, 3 were bimodal, and 5 were active throughout the day (Fig. 3). Three of the large male *H. texana* were seen on 60–70% of the days but the remainder were only seen on 15–40% of the days. Of the 13 *U. stansburiana*,

5 were active only in the morning, 4 were active only in the afternoon, and 4 were bimodal (Fig. 4). The three *P. modestum* and three *S. magister* were bimodal. Three *P. cornutum* were active only in the morning, one was active only in the afternoon, and one was bimodal. Two *C. tessellatus* were morning active only and one was active only at midday. Of the four *C. wislizenii*, two were bimodal, one was morning active, and one was afternoon active.

In previous studies (Whitford and Creusere 1977) we noted that the number of individuals observed hourly seldom exceeded 25% of the population based on mark-recapture estimates. When we increased the number of observers to six and walked a 60-m-wide transect across the site, we improved only slightly; 35% of the estimated population was observed. Previous pitfall trap data for 1970-74 indicated that many individuals were captured several times in one area followed by several weeks without recapture before being taken again in that area. We initially assumed that these lizards foraged in adjacent areas for a period of time before returning to the trapping grid. However, frequent sightings of individuals were followed by periods with no sightings on either the grid or buffer zone, which suggests these animals may have been aestivating. Some individuals of all species remained active throughout the summer.

The individuals that had short periods of activity were feeding during most of that period. Lizards with more extended activity periods fed in short spurts throughout the activity period, spending the remainder of the time at rest on the surface.

Spatial Patterns

To adequately interpret the temporal activity patterns of individual lizards, it is necessary to examine their spatial distribution. There was little spatial overlap in the species occurring at low densities, and here we present data only for *C. tigris* and *H. texana*.

The overlap of male and female *C. tigris* was almost complete (Fig. 5). Of the area occupied by males, 47% was used by only one male, 37% by two, 11% by three, and 5% by four. The average number of individuals using a given point within all the male activity areas was 1.7. Maximum overlap values for male *C. tigris* are

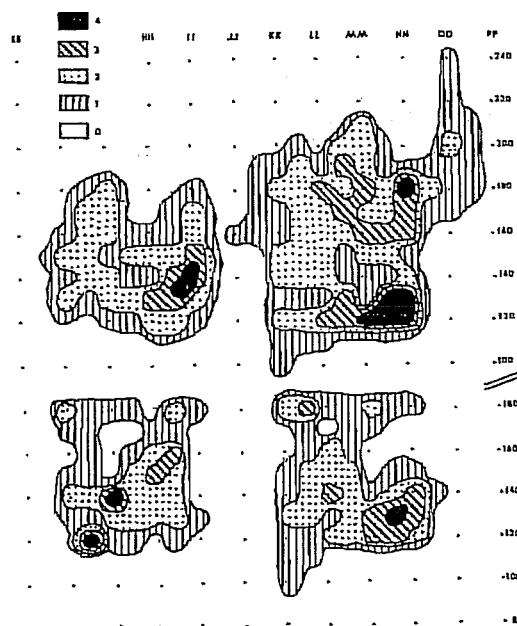


Fig. 5. Spatial overlap in *Cnemidophorus tigris*. The upper plots are for males and the lower plots for females. Different patterned areas indicate use by zero to four individuals of the same sex. Grid points are 20 m apart.

as follows: 1.00 overlap with at least one other male, 0.90 with at least two other males, and 0.50 with three or four other males (i.e., one male's activity area was completely contained in the areas of other males, 90% of one male's activity area fell into areas used by two or more other males, and 50% of one male's activity area was used by at least three other males).

Female use of space was similar: 51% of female activity areas was used by only one, 35% by two, 11% by three, and 4% by four. The average number of females using a given part of an activity area was 1.7—the same as for males. Maximum overlap for female activity areas was 0.81 with one or more other females, 0.45 with two or more others, and 0.45 with three or four others.

Among male *H. texana*, the maximum observed overlap was 0.62 with at least one other male, 0.50 with two or more others, and none overlapped with three others. There was virtually no overlap in *H. texana* females; the maximum overlap for any female activity area was 0.12 with one other.

In spite of overlaps, we almost never observed more than one individual of a species in proximity to another of the same species.

During the few weeks when both adults and juveniles were active, the adults tended to remain in the vicinity of denser vegetation and juveniles appeared to be relegated to more open vegetation. For example, adult *H. texana* were usually found in large arroyos having $> 1 \text{ m}^2$ of open stream bed, some rocks, and dense clumps of apache plume at the edge. Juvenile *H. texana* were found in the open upland areas of creosotebush until the adults ceased activity late in the season. The juveniles then migrated to the arroyos.

Discussion

The most intriguing result of these studies is that in the most numerous species individual lizards exhibited consistent but abbreviated patterns of activity. Many individuals in the population do not overlap temporally although these same individuals may overlap spatially. This temporal separation reduces intraspecific competition and increases carrying capacity probably by increasing feeding efficiency. This seems particularly likely in *C. tigris*, which occurs at densities of 30–40/ha (Whitford and Creusere 1977) and which have home ranges of about 0.57 ha (range 0.1–2.4 ha) in this study. *Cnemidophorus tigris* feed primarily on termites (Pianka 1970) by rooting through accumulations of leaf litter. Although a morning feeder would disturb the termites and remove a small number, the subterranean galleries of the termites would be left undisturbed. If the litter is in a shaded, temperature-moderated area, the termites will reenter within a few hours (Johnson and Whitford 1975; W. G. Whitford, personal observation). Thus, individual lizards active at different times of the day could feed in the same location. Even at densities of 30–40/ha, *C. tigris* is not likely to deplete the termite population which we estimate conservatively to exceed 1,200/m² (Johnson and Whitford 1975). With a food resource as large and temporally flexible as termites, *C. tigris* can exist at high densities avoiding intraspecific competition by utilizing the same space at different times of the day.

Simon and Middendorf (1976) presented the

only recorded example of spatial and temporal overlap in a single species of lizard and stated that little overlap has been described in any taxon. Here we document temporal and spatial overlap in *C. tigris* and *H. texana*. We suggest that such overlap may be the rule rather than the exception, particularly in species that achieve high densities. There are many species of organisms that use extremely abundant food resources and that occur at densities that should result in considerable intraspecific competition because of spatial overlap. Intraspecific interactions are energy expensive and, if agonistic, can be damaging. There appears to be remarkable lack of intraspecific agonistic behavior in harvester ants (Whitford 1976), and in *C. tigris* and *H. texana* as documented in this study. It seems likely that temporal separation could be behaviorally established early in a season and maintained throughout the season.

Spatial overlap of a male and female in sexually reproducing species is expected, but spatial overlap of several males is not. The relation between lizard body size and extent of activity suggests the behavioral establishment of a temporal hierarchy. In *H. texana*, the largest lizards exhibited the all-day pattern of activity. The smaller lizards had the more temporally restricted activity pattern. This could be interpreted as dominant-subordinate interaction; the subordinate is relegated to less favorable foraging times. The peak activity of ground and litter arthropods is in the early morning and evening when temperatures near the ground are more favorable for their activity (W. G. Whitford, unpublished data). Larger lizards may have to spend more time active on the surface to maintain body temperatures at preferred levels for digestion and other physiological processes, and they may require a longer time to fill their stomachs. This need for an extended feeding-digestion period seems to be a reasonable explanation for the body size-activity pattern in *H. texana*.

It is apparent from this study that individual lizards are not surface active every day; the data suggest that most are active about 2 days per week or less. Simon and Middendorf (1976) found that *Sceloporus jarrovi* were active on the average only 2.5 days per week. Even allowing for large errors in our data due to the limitations of the walking transect technique, we can state with confidence that individual lizards were ac-

tive less than 50% of the time with the few exceptions noted in *H. texana*. Considering a pattern of surface activity that is less frequent than daily and the reduced diel activity patterns of individual lizards, it is apparent that temporal partitioning is much more important than previously thought (e.g., Schoener 1974) and deserves further investigation to see if this results in a partitioning of food resources.

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Use of Cave Resources by a Lizard Community

by

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Abstract

A community of three lizard species exploits the resources of a system of caves at Puerto Marquez, Guerrero, Mexico. The caves provide a stable, low-temperature, high-humidity environment with variable and sparse food resources. *Anolis taylori*, *Phyllodactylus lanei*, and *Lepidophyma smithi* differ in the degree to which they utilize the cave resources. These differences are apparent in activity pattern, body temperature, evaporative water loss, and diet. Adaptations for cavernicolous life involve absence of a diel activity cycle, absence of thermoregulatory activity, low resistance to water loss, and a generalized diet that, at Puerto Marquez, includes decaying fruit and probably carrion.

Cave communities are distinctive in that they contain no photosynthetic autotrophs (Barr 1967, 1968; Poulson and White 1969). The food web within a cave is based on detritus which is transported from the outside by flooding or animal movements. Cavernicolous animals must therefore be adapted to food resources that are often scarce, of little nutritive value, or sporadic in availability. As a consequence of these energetic restrictions, the subterranean community is greatly simplified compared to its epigeal counterpart, both in terms of lower species richness and standing crop biomass. Caves are buffers to changes in the outside climate. Temperature is stabilized at very near the average yearly epigeal temperature, and humidity is high and stable. The magnitude and lag of fluctuations depend on how open the system is, which in turn depends on the size, number, and exposure of entrances, and the distance from the entrances (Poulson 1964).

Most cavernicolous vertebrates are facultative although a small number of salamanders and fishes are obligate cave inhabitants. Few lizards are associated with cave communities. Xantusiid lizards of the genus *Lepidophyma* have been found in caves (Walker 1955; Smith and Alvarez

del Toro 1977) but little is known of the biology of these species.

I report here on the use of a cave system in southern Mexico by three species of lizards: *Anolis taylori*, *Phyllodactylus lanei*, and *Lepidophyma smithi*. Different degrees of adaptation to cavernicolous life are shown in comparisons of the activity patterns, thermoregulation, water loss, and diet of these species.

Materials and Methods

Observations were made in August 1973, July 1974, and January and November 1976, at a site 2 km west of Puerto Marquez, Guerrero, Mexico. Caves in this region are formed by large granitic boulders that are piled in ravines draining steep hillsides. The boulder aggregations produce a system of caves with multiple entrances and extensive twilight zones grading to complete darkness in the deeper recesses (Fig. 1). This unique structure permits input of detritus and provides access to animals over a large surrounding area. The surface vegetation is a semideciduous tropical forest. Average monthly temperatures range from 26° to 29°C and average annual rainfall is 1,400 mm, nearly all of which falls between May and October (Instituto de Geographica, Universidad Nacional Autonoma de Mexico).

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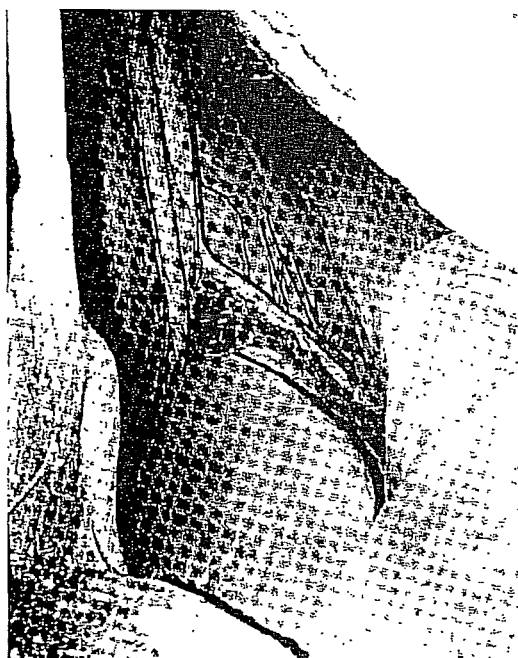


Fig. 1. Interior view of a cave at Puerto Marquez, Guerrero, Mexico. Roots of fig trees, *Ficus petiolaris*, entwine boulders and penetrate to soil below. The boulder in the lower center of the photograph is about 1 m in diameter.

Measurements of temperature and humidity in the cave twilight zone and forest floor environments were made with a sling psychrometer held 1 m above the substrate. Lizard body temperatures were measured within seconds of capture by cloacal insertion of a Schultheis rapid registering mercury thermometer. All thermometers were calibrated against a National Bureau of Standards certified mercury thermometer; humidities were calculated from List (1949). Lizard activity was determined by direct observation and trapping (Mautz and Lopez-Forment 1978). Evaporative water loss was measured in the field by direct weighing. Lizards were placed in plastic boxes 10 cm on a side with screen floors over a layer of mineral oil. The boxes were roofed with additional screen to permit equilibration with the stabilized microclimate of the cave. Lizards were weighed to 0.01 g every 24 h. Fecal masses were collected and stored under oil for determination of water content by the method of

Minnich and Shoemaker (1972). Water loss data from animals that defecated were discarded. A series of animals were collected for analysis of gut contents.

Results

The diel variation in temperature and vapor density deficit is plotted in Fig. 2 for sites both inside and outside the caves during wet and dry seasons. Vapor density deficit is the difference between the concentration of water vapor in the air and the saturation concentration of water vapor at the air temperature. It is a measure of the evaporating potential of the air; high values of vapor density deficit represent a high evaporation potential. During both wet and dry seasons, the cave environments maintained a steady and low temperature and vapor density deficit, cycling between 24° and 27°C and 2 to 5 g/m³, respectively. Organisms in the cave environment enjoy the benefits of a reduced evaporation potential, but must contend with a temperature regime which, while stable, is relatively low.

The three species of lizards differ markedly in the time spent and the activities performed in the caves. The iguanid, *Anolis taylori*, moves into the caves shortly before sunset and is inactive through the night. These lizards cling to open vertical surfaces and do not seek the close confines provided by thin crevices within the caves. This behavior may minimize the risk of predation by large scorpions and amblypygids, which frequent fissures in the cave walls. The anoles do not penetrate to the dark zone of the caves at any time during the night. At dawn they move to the surface to forage and bask. The gekkonid, *Phyllodactylus lanei*, can be found on the walls and in crevices within caves by night or day; it is also found on the surface outside of caves from shortly after sunset to midnight. Ten specimens collected from the surface all had food in their stomachs. Four of these contained intact arthropods, indicating that the lizards forage on the surface at this time. The xantusiid, *Lepidophyma smithi*, is found only within caves. Individuals were located by night and day within crevices and on the walls, and they were captured in equal frequencies by day or night in traps baited with fish (Mautz and Lopez-Forment 1978). *Lepidophyma smithi*

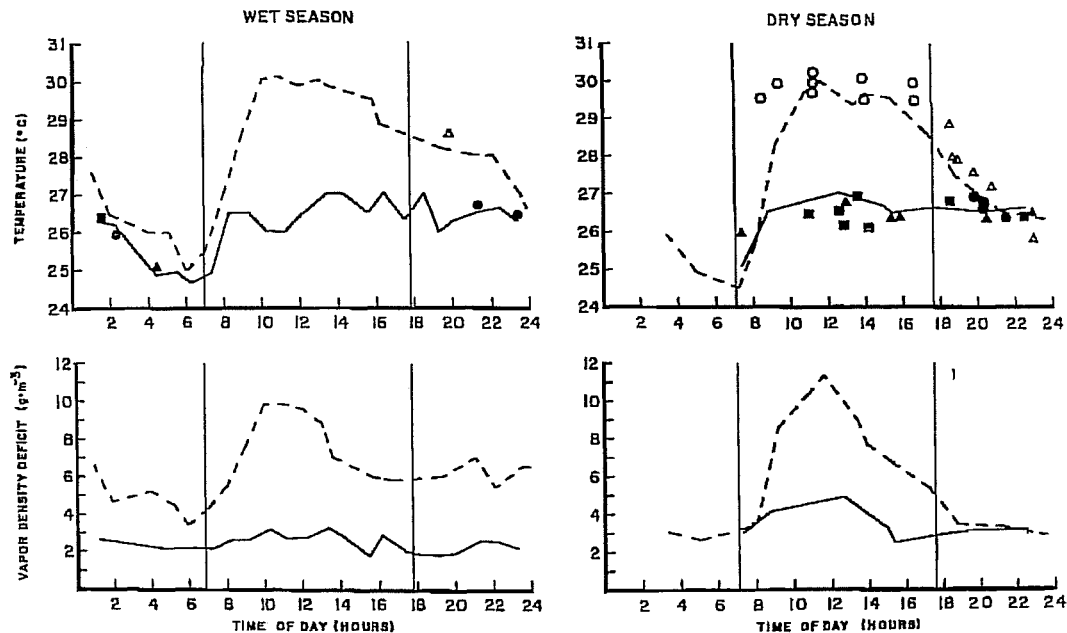


Fig. 2. Microclimate variation and lizard body temperatures at Puerto Marquez, Guerrero, Mexico. Dashed lines are air temperature and vapor density deficit outside of caves, solid lines are inside caves; open symbols are lizards outside caves, solid symbols are lizards inside caves; circles (○, ●), *Anolis taylori*; triangles (△, ▲), *Phyllodactylus lanei*; and squares (■), *Leptidophyma smithi*. Thin vertical lines indicate time of sunrise and sunset. Wet season data were collected 7–8 July 1974, and dry season data were collected 28–29 November 1976.

thus appears to forage without a diel activity cycle.

Temporal and spatial differences in the activity of these lizard species are correlated with their body temperatures (Fig. 2). By day, *A. taylori* frequents tree trunk and ground microhabitats where it basks in the early morning and late afternoon, elevating its body temperature to 30°C. During midday, the air temperature is sufficiently high for the lizards to maintain activity temperatures without basking. Shortly before sunset the lizards move into the openings of the caves and assume sleeping positions; their body temperatures then closely approximate cave air temperature. *Phyllodactylus lanei* exhibits two kinds of body temperature cycle depending on whether the animals emerge or remain in caves in the evening. Animals remaining in caves have body temperatures equal to cave air temperature. Emergent animals achieve evening body temperatures higher than outside air temperature by heat conduction from boulder surfaces warmed earlier

by sunlight. Later at night large areas of the boulder surfaces exposed to the night sky may cool by radiant heat loss to levels below air temperature. The low body temperature of a *P. lanei* at 2300 h on 29 November (dry season data, Fig. 2) is probably a result of contact with an exposed boulder surface from which it was collected. Since *L. smithi* do not leave the caves, their body temperatures consistently equal cave air temperature.

Rates of water loss in milligrams H_2O/g per h of the three lizard species (Table 1) do not differ significantly ($F = 0.48$); however, differences in the body weight and activity of the animals obscure physiological differences in their resistance to water loss. *Leptidophyma smithi* is nearly three times as massive as the other species, but its surface area, estimated by $SA = 10 \cdot W^{2/3}$ (Benedict 1932), is less than twice that of the others. Thus the conductance of water vapor for *L. smithi*, expressed per unit of surface area instead of per unit mass, is higher. The reciprocal of conductance, resistance, will be correspon-

Table 1. *Evaporative and excretory water loss of Anolis taylori, Phyllodactylus lanei, and Lepidophyma smithi. Values are means \pm standard errors.*

Species	Body weight		Evaporative water loss		Water content of excreta	
	No. of specimens	g	No. of specimens	mg/g per h	No. of specimens	% wet weight
<i>Anolis taylori</i>	7	6.9 \pm 0.73	7	1.01 \pm 0.08	6	70 \pm 3
<i>Phyllodactylus lanei</i>	5	5.9 \pm 0.03	5	1.26 \pm 0.34	1	67
<i>Lepidophyma smithi</i>	5	17.5 \pm 2.41	5	1.12 \pm 0.08	13	65 \pm 2

dingly lower than that for the other species. Therefore, *L. smithi*, the species with the strongest affinity for caves, has the lowest resistance to water loss. Furthermore, there is great variation in activity among the lizard species. *Lepidophyma smithi* is a sedentary lizard which rarely moves from perch sites within caves. Emerging *P. lanei* are slightly more active; individuals typically make short excursions interspersed by long periods of inactivity. In contrast, *A. taylori* makes short rapid movements over boulders and tree trunks with considerable frequency. These activity patterns were also reflected in the behavior of the animals during water loss measurements. *Lepidophyma smithi* and *P. lanei* remained motionless whereas *A. taylori* often jumped at the sides of the containers. Animal activity is rarely controlled in studies of water loss, but it does exert a marked effect on evaporation (Gans et al. 1968; Dmi'el 1972; Mautz 1980). The activity of the *A. taylori* probably elevated its water loss rates above resting levels; it is likely that physiological resistance to water vapor flux at rest is higher in this species. The other avenue of water loss is excretion and all three species appear to lose the same proportion of water in feces and urates (Table 1).

The diets of *A. taylori* and *P. lanei* consist of a variety of small arthropods, but *L. smithi* feeds almost entirely on *Ficus* fruit that falls or washes into the caves.

Discussion

Cavernicolous organisms inhabit an environment of darkness, low temperature, high humidity, and biotic simplicity. Differences in the extent to which these organisms occupy caves and are restricted to them are reflected in

a gradation of adaptations to the cave environment. Obligatory cave existence is not known among lizards, but species that are secretive or nocturnal possess some of the appropriate adaptations—characteristics which are "protoadaptations" for cavernicolous life. These species are able to utilize caves to different degrees. Lizards found in the caves at Puerto Marquez exemplify such a gradation in adaptations and, in correspondence, a gradation in involvement in the cave community. In the absence of physiological tolerance to low temperature, heliothermic iguanids like *A. taylori* will be excluded from cave habitats except during the inactive phase of their daily cycle. Some other *Anolis* species are not heliotherms and their body temperatures passively follow air temperature (Hertz 1974; Huey 1974; Huey and Webster 1976). Thermal constraints alone are insufficient to exclude such eurythermic iguanids from caves. Gekkonids and xantusiids have low activity temperatures (Brattstrom 1965; Mautz and Case 1974; Pianka and Pianka 1976). These are compatible with the warmer caves in tropical and subtropical climates. *Phyllodactylus lanei* achieves elevated body temperatures during the brief interval of evening emergence. This may be an important component of the thermal biology of these animals in that it enhances digestion at a time when the lizards are foraging (Regal 1966). *Phyllodactylus lanei* and *L. smithi* exhibit no thermal or activity characteristics peculiar to their families except for the apparent lack of a diel activity cycle in *L. smithi*. The temperate xantusiids, *Xantusia henshawi*, *Xantusia vigilis*, and *Klauberina riversiana*, possess diel activity cycles (La Pointe 1967; Regal 1967; Lee 1974; Mautz and Case 1974). The lack of rhythmicity in *L. smithi* may not be unique, as no one has studied the activity of other *Lepidophyma* species in lowland tropical climates where tem-

peratures may be suitable for nocturnal and diurnal activity.

Environmental determinants of evaporative water loss also differ between cave and epigeal habitats. Lower temperature and water vapor density deficit in the caves produce an environment in which evaporation will be reduced. If other factors influencing the water budget of lizards were equal, one would expect a reduced physiological resistance to evaporation in cavernicolous species, which would be reflected by high water loss rates for these animals. Other factors were not equal among the three species studied and physiological resistance to evaporation was not directly measured, but a number of inferences can be drawn from the evaporative water loss measurements. The rates at which the tissues of the three species desiccate by evaporation (mg/g per h), the water content of excreta, and thus the rate at which lizards must replenish lost water are equal. It appears that the sources of water for these lizards, largely water in food and freestanding drinking water, are similar. Differences in the resistance to water loss of these species are implied by differences in body size and activity. *Lepidophyma smithi* is a much more massive animal with a correspondingly lower surface to mass ratio, and the resistance to water loss across its surface must be much reduced to produce a desiccation rate equivalent to the other smaller species. *Anolis taylori* and *P. lanei* are similar in size but differ markedly in activity. The equivalence of desiccation rates in these species implies a reduced resistance for the sedentary gekkonid compared to the active iguanid. It appears that physiological resistance to water loss may be adjusted to compensate for the differing effects of body size, activity, and environment.

Probably the greatest challenge to lizards inhabiting caves is the scarcity of quality food resources. At Puerto Marquez, *A. taylori* does not forage inside the caves, and a large proportion of the population of *P. lanei* also forages on the surface. The omnivorous diet of *L. smithi* admirably suits these lizards to life entirely within these caves. They find the bulk of their food among the detritus that falls and washes into the caves and supplement this diet with occasional arthropod prey and probably carrion. Nothing is known of the diet of other *Lepidophyma* species, but another large xantusiid, *Klauberina riversiana*, has a generalized, omnivorous diet

(Knowlton 1949; Schwenkmeyer 1949). It is therefore likely that other large species of *Lepidophyma* are at least partially herbivorous.

Many lizards may be protoadapted for occupying caves because they are tolerant of low temperature, low light levels, and scarce or nutrient-poor food. *Anolis taylori* is ill equipped for these typical cave conditions and consequently it uses caves only as a nocturnal retreat. *Phyllodactylus lanei* is better adapted for living in caves but emerges to forage at night. *Lepidophyma smithi* can remain within caves continuously although it probably is not restricted to caves. The adaptations of the latter two species are effective in suitable epigeal habitats as well, and are also present in other nocturnal and secretive members of their families which do not live in caves.

Acknowledgments

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Structure and Composition of Mojave Desert Reptile Communities Determined with a Removal Method

by

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Abstract

Species diversity, relative abundance, and biomass were determined by a removal method for communities of diurnal reptiles (lizards and tortoises) in creosote-shrub habitat in the western Mojave Desert, California. Collecting on 2 consecutive days (3 h in late morning) proved effective in sampling the fauna. Four to six species occurred at each site; the species diversity indices varied little between sites. Three species of lizards made up 83 % of the individuals in the sample: *Callisaurus draconoides*, *Cnemidophorus tigris*, and *Uta stansburiana*. The desert tortoise, *Gopherus agassizii*, constituted 80 % of the estimated biomass. Of the remaining biomass, 84 % was contributed by *Cnemidophorus tigris*, *Callisaurus draconoides*, and *Phrynosoma platyrhinos*.

Descriptions of reptile communities should include measures of species diversity, abundance, and estimated biomass because all of these variables help to delineate the importance of certain components and indicate relations in communities. For example, *Gopherus* was numerically uncommon in the present study but because of its large size it is an energetically important herbivore in creosote-shrub habitat.

No sympatric congeners occurred in the study sites. All of the reptiles appeared to be broadly different in food habits or microhabitat, or both, which reduces interspecific competition.

Most research on North American desert reptiles has focused on autecological studies, e.g., the biology of *Sceloporus magister* (Tinkle 1976); *Crotaphytus wislizenii* (Turner et al. 1969a; Tanner and Krogh 1974; Parker and Pianka 1976); *Phrynosoma platyrhinos* (Medica et al. 1973; Pianka and Parker 1975); *Callisaurus draconoides* (Kay 1970; Pianka and Parker 1972; Tanner and Krogh 1975); *Cnemidophorus tigris* (Medica 1967; Turner et al. 1969b; Pianka 1970; Parker 1972); *Uta stansburiana* (Tinkle 1967; Turner et al. 1970); *Dipsosaurus dorsalis* (Krekorian 1977); and *Gopherus agassizii* (Engberg et al. 1976). These studies provide important comparative data on single species.

Studies on sympatric species of desert lizards are few but explore important aspects of com-

munity structure. Pianka (1967, 1973, 1975) investigated species diversity and niche relations of North American desert lizards. Whitford and Creusere (1977) and Creusere and Whitford (this volume) reported on temporal changes in a Chihuahuan Desert lizard community.

The present study employed a removal method to analyze the species diversity, density, and biomass of diurnal reptiles in creosote-shrub habitats in the Mojave Desert. These measures were used to better define the structure and composition of desert reptile communities.

Materials and Methods

In 1974 and 1975, field studies were conducted at four undisturbed localities in San

Table 1. *Lizards and tortoises taken on 2 days (6 man-hours/ha) on 2-ha sites, western Mojave Desert, California.*

Site	Number of species	Number of individuals	Species diversity index	Total biomass (g/2 ha)	Lizard biomass (g/2 ha)
Barstow					
A	6	57	1.39	3,189	643
D	5	60	1.26	4,597	737
Stoddard Wells					
E	5	54	1.27	490	490
G	5	46	1.48	509	509
Anderson Valley					
K	6	26	1.59	1,480	480
L	5	31	1.46	9,023	348
Johnson Valley					
M	4	46	0.94	474	474
N	6	53	1.14	1,080	580

Bernardino County, California, in the upland portion of the western Mojave Desert. Two sites of 2 ha each were sampled at the four localities, for a total sample area of 16 ha. All study sites were between 740 and 1,100 m in elevation and were dominated by creosotebush (*Larrea tridentata*, \bar{x} = 240 shrubs per ha, range 153–328). The study sites are described elsewhere (Bury et al. 1977).

The rationale for, and development of, the removal sampling techniques to estimate population size were described by Zippin (1956, 1958) and Delany (1974). I found that this method was an effective sampling technique for measuring diurnal reptile populations (Busack and Bury 1974; Bury et al. 1977). In earlier work, I expressed population size as the total sample collected, and I follow this method here to facilitate comparisons. Measures of species diversity, abundance, and biomass were calculated from the total of all animals taken. A similar standardized procedure was used to study desert rodents (Brown 1973, 1975; Brown and Lieberman 1973).

The removal method consisted of systematic, repeated search of established quadrats (100 × 200 m); collection was by shooting with elastic bands or .22 dust shot, and by hand-capture. Two collectors sampled halves of the 2-ha sites simultaneously (from 0900 to 1200 h) and exchanged halves daily to reduce collecting bias. Searching was done from late April to early

June, the peak periods of surface activity for diurnal reptiles in the Mojave Desert.

The minimum sampling period was 3 h/day for 2 days. Comparisons were made on data obtained from the first 2 days of sampling at all eight sites. A third sampling day of 2 h was obtained at six of these sites. These data were used in the discussion of sampling methods.

All animals were removed from the quadrats, sexed, measured, and weighed (to the nearest 1 g or, for small reptiles, 0.1 g). Animals killed were prepared as museum specimens. Protected forms (*Gopherus*, *Phrynosoma*, *Crotaphytus*) were measured and released alive at the place of capture.

Three snakes (*Pituophis*, 450 g; *Masticophis*, 250 g; and *Sonora*, 8 g) were found on the sites. They were not included in the data analysis. Other sampling techniques are needed to accurately estimate the number of snakes present. In the results and discussion that follow, "reptiles" refers to lizards and tortoises only.

Results of Removal Sampling

Use of the removal sampling technique provided estimates of relative occurrence (species diversity), abundance (number per unit area), and biomass (weight per unit area) (Table 1). The majority of individual reptiles were taken on the first day (Fig. 1, Fig. 2a). The average

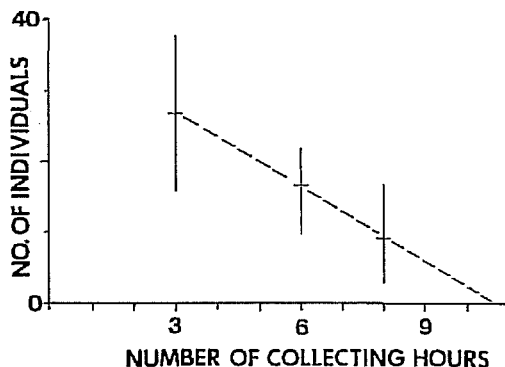


Fig. 1. Number of individuals of diurnal lizards and tortoises removed on 3 successive days from Mojave Desert sites ($N = 5$). Vertical bars are ranges and horizontal bars are means. Dashed line is fitted by eye.

number of reptiles obtained per day declined steadily from Day 1 to Day 3.

The average number of species per site were Day 1, 5.4; Day 2, 4.0; and Day 3, 2.6. New species were added on only two of the eight sites on the second day of sampling (one *Dipsosaurus dorsalis* at site N, one *Callisaurus draconoides* at site E) (Fig. 2b). No additions were made on the third day. Thus the removal method revealed almost all the resident diurnal reptile species in two sampling days. There may be some uncommon or peripheral species that will be found only with long searches, but the species composition of desert diurnal reptiles evidently can be effectively determined in 2 days by the removal technique.

The cumulative weights of reptiles captured were not noticeably increased with further hours of collecting (Fig. 2c). This was principally due to the large weights of desert tortoises (*Gopherus agassizii*), which were generally found on Day 1 because they were conspicuous and usually easy to locate if burrows were carefully searched. Similarly, the greatest lizard biomass was recorded on Day 1 (Fig. 2d).

Species Diversity

The number of species collected on the first 2 days at each of the eight sites varied from four to six ($\bar{x} = 5.3$). The Shannon and Weaver (1963)

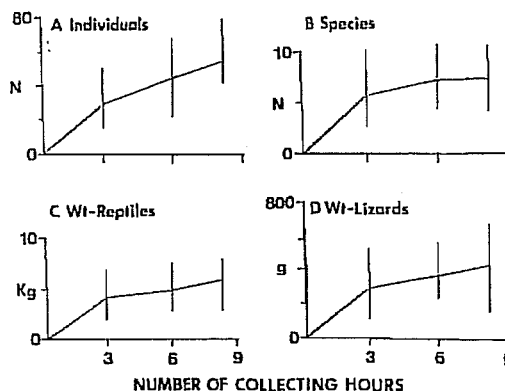


Fig. 2. Cumulative totals of (a) numbers of individuals, (b) numbers of species, (c) weights of diurnal lizards and tortoises, and (d) weights of diurnal lizards alone, obtained over 3 days (3:3:2 h periods) on eight 2-ha sites in the Mojave Desert. Vertical bars are ranges and solid lines connect means.

Index was used to compare species diversity. Little difference between the sites was found; index values were from 0.94 to 1.59 (Table 1).

Callisaurus draconoides, *Cnemidophorus tigris*, and *Uta stansburiana* occurred on all study sites (Table 2). *Phrynosoma platyrhinos* was found on six sites. Both *Sceloporus magister* and *Dipsosaurus dorsalis* were recorded on only one quadrat; the populations of these relatively heavy-bodied lizards were lower on the study sites than in other habitats. The sites had few suitable habitats for those lizards: few or no trees and little sandy soil. I found *Sceloporus magister* at Stoddard Wells, where there were a few scattered Joshua trees (*Yucca brevifolia*). The one *Dipsosaurus* I found was in Johnson Valley, where some sandy areas occurred.

Urosaurus graciosus, a shrub- or tree-dwelling form, was not found in the study areas, but this species frequents creosote habitat elsewhere. *Coleonyx variegatus* probably was present, but the nocturnal lizard fauna was not sampled. *Xantusia vigilis* also probably occurred at many sites, but special collecting efforts (raking through surface debris) are needed to find these lizards.

Composition of Herpetofauna

Three species of lizards made up 83% of the reptiles sampled (Table 2); *Callisaurus draco-*

Table 2. Number and percentage of individuals taken on 2 days (6 man-hours/ha) at eight 2-ha sites, Mojave Desert, California. Figures in italics are the percentage of individuals at each site.

Species	Barstow		Stoddard Wells		Anderson Valley		Johnson Valley		Total
	A	D	E	G	K	L	M	N	
<i>Callisaurus draconoides</i>	5	28	1	10	6	8	31	33	122
	8.8	46.7	1.8	21.7	23.1	25.8	67.4	62.3	32.7
<i>Cnemidophorus tigris</i>	27	18	19	8	9	7	9	8	105
	47.4	30.0	35.2	17.4	34.6	22.6	19.6	15.1	28.2
<i>Uta stansburiana</i>	15	8	19	15	5	10	3	8	83
	26.3	13.3	35.2	32.6	19.2	32.3	6.5	15.1	22.3
<i>Phrynosoma platyrhinos</i>	5	—	13	11	2	—	3	2	36
	8.8	—	24.1	23.9	7.7	—	6.5	3.8	9.6
<i>Gopherus agassizii</i>	4	5	—	—	1	5	—	1	16
	7.0	8.3	—	—	3.9	16.1	—	1.9	4.3
<i>Crotaphytus wislizenii</i>	1	1	—	2	3	1	—	—	8
	1.7	1.7	—	4.4	11.5	3.2	—	—	2.1
<i>Sceloporus magister</i>	—	—	2	—	—	—	—	—	2
	—	—	3.7	—	—	—	—	—	0.5
<i>Dipsosaurus dorsalis</i>	—	—	—	—	—	—	—	1	1
	—	—	—	—	—	—	—	1.9	0.3
Totals	57	60	54	46	26	31	46	53	373

noides was the most common species (33%), followed by *Cnemidophorus tigris* (28%), and *Uta stansburiana* (22%). *Phrynosoma platyrhinos* made up about 10% of the individuals found. The three other lizard species combined constituted less than 3% of the fauna; *Gopherus* was also a numerically minor part of the samples (4%).

There was considerable variation in the frequency of different lizards at different sites. At Barstow, about half of the lizards at site A was *Cnemidophorus*, whereas at site B about half was *Callisaurus*. *Uta* and *Phrynosoma* were most frequent at Stoddard Wells, and both sites in Anderson Valley had high proportions of *Cnemidophorus*, *Callisaurus*, and *Uta*. The Johnson Valley sites had exceptionally high numbers of *Callisaurus*.

Cnemidophorus was found in much larger numbers than *Callisaurus* at two sites (A, E) whereas the reverse was true at three sites (D, M, N), but the negative correlation between the numbers of these two species on the eight sites is not statistically significant ($r_s = -0.50$, $P > 0.05$). These data suggest that these two species probably do not exclude one another.

Biomass

The large differences in total weights of rep-

tiles between sites (Tables 1 and 3) were due largely to the uneven representation of the large-bodied tortoises. The tortoises alone constituted about 80% of the estimated biomass of the diurnal reptile community. The three commonest lizards made up only 16% of the total weight of the sampled fauna. The rank order of the contribution of each lizard species to the total biomass was as follows: *Cnemidophorus tigris*, *Callisaurus draconoides*, *Phrynosoma platyrhinos*, *Crotaphytus wislizenii*, and *Uta stansburiana*. Other lizards each contributed less than 1% (Table 3).

The distribution of lizard biomass was different from the proportion of individuals of each species. In both weight and numbers, *Callisaurus* and *Cnemidophorus* constituted the major segment of the lizard fauna (Tables 3 and 4). *Phrynosoma* and *Crotaphytus* were low in numbers, but when present they contributed appreciably to the total biomass. The numerically common *Uta* contributed a minor part of the total biomass because individual weights were only 2–3 g.

Discussion

I used the removal method on a total of 28 study sites; on 8 plots (16 ha) of undisturbed creosote-shrub habitat (present report), on 8 plots

Table 3. *Estimated biomass (in g per 2 ha) for tortoises and lizards at eight 2-ha sites, Mojave Desert, California. Percentage composition is in italics.*

Species	Barstow		Stoddard Wells		Anderson Valley		Johnson Valley		Total
	A	D	E	G	K	L	M	N	
<i>Gopherus agassizii</i>	2,545	3,860	—	—	1,000	8,675	—	500	16,580
	79.8	84.0			67.8	96.1		46.3	79.6
<i>Cnemidophorus tigris</i>	353	369	219	162	237	175	159	139	1,813
	11.1	8.0	44.7	31.8	16.0	2.0	33.5	12.9	8.7
<i>Callisaurus draconoides</i>	43	317	21	105	102	103	276	301	1,268
	1.4	6.9	4.3	20.6	6.9	1.2	58.2	27.9	6.1
<i>Phrynosoma platyrhinos</i>	122	—	117	128	51	—	32	36	486
	3.8		23.9	25.2	3.4		6.8	3.3	2.3
<i>Crotaphytus wislizenii</i>	75	28	—	62	76	39	—	—	280
	2.3	0.6		12.2	5.1	0.4			1.3
<i>Uta stansburiana</i>	51	23	53	52	14	31	7	23	254
	1.6	0.5	10.8	10.2	1.0	0.3	1.5	2.1	1.2
<i>Dipsosaurus dorsalis</i>	—	—	—	—	—	—	—	81	81
								7.5	0.4
<i>Sceloporus magister</i>	—	—	80	—	—	—	—	—	80
			16.3						0.4
Totals	3,189	4,597	490	509	1,480	9,023	474	1,080	20,842

(16 ha) of nearby disturbed land (Bury et al. 1977), and on 12 plots (24 ha) of sand dune habitat, half of which was damaged by off-road vehicles (R. B. Bury, unpublished data). I have also modified the method for censusing tortoise populations on two 25-ha plots in the Mojave Desert (Bury and Luckenbach 1977).

Most knowledge on desert reptiles has been obtained by intensive work at one or a few study areas, the approach typical of most research on desert reptiles; however, better comparative data may be available by extensive sampling at many sites. I suggest that the removal sampling technique is a promising tool for use in extensive surveys and population studies because it is an effective system to assess diurnal reptile communities.

Collecting efforts were most efficient (animals/hour effort) on the first day and somewhat less on the second day (Fig. 1). Few were found on subsequent searches. I suggest that a 2-day period (3 h/site per day) be used because collecting was still efficient on Day 2 and the second day appreciably increased the sample sizes (Figs. 1 and 2). Continued sampling apparently does not contribute enough additional information to justify the extra effort. Also, there are increased chances of emigration into the plots with longer sampling periods.

Workers may also want to try a thorough 1-day search (4 h in the morning, 2 h in the late afternoon or evening) or a 2-day regime of 4 h each day. Where animals may be shot, I believe that one collector can effectively search 2 or per-

Table 4. Percentage composition of biomass of the lizard fauna taken on 2 days at eight 2-ha sites, Mojave Desert, California.

[illegible]

haps 3 ha of creosote habitat in a 4-h period. Catchability of reptiles and local variables may alter the technique's effectiveness. For example, I found that two collectors can more efficiently locate fringe-toed lizards (*Uma*) than a single worker.

Pianka (1967) reported that four species of lizards are ubiquitous throughout the deserts of the western United States: *Cnemidophorus tigris*, *Uta stansburiana*, *Crotaphytus wislizenii*, and *Phrynosoma platyrhinos*. Eight other species are variously added in the southern parts of these deserts but more than 10 diurnal species are not known in any area. In the Mojave Desert, Pianka estimated that seven to nine species of flatland lizards were present. If I assume that *Xantusia vigilis*, a crepuscular species, and *Coleonyx variegatus*, a nocturnal form, were present on my study sites, the number of species in the creosote-shrub areas closely corresponds with Pianka's (1967) estimates.

The creosote-shrub community in the Mojave Desert is typified by five lizards (*Callisaurus draconoides*, *Cnemidophorus tigris*, *Uta stansburiana*, *Phrynosoma platyrhinos*, and *Crotaphytus wislizenii*) and the desert tortoise (*Gopherus agassizii*). Species diversity measures would be increased by the inclusion of nocturnal reptiles or species inhabiting other habitats such as sandy soils (*Dipsosaurus dorsalis*, *Uma* sp.) and rocky terrain (*Sauromalus obesus*, *Crotaphytus collaris*, *Sceloporus magister*). *Sceloporus magister* also occurs in a wide range of conditions and frequents areas with trees or tall shrubs in the Mojave Desert. *Urosaurus graciosus* is a shrub dweller in some areas of creosote. These assemblages may be found together where their habitats come into contact or interdigitate, and as many as 12 species of diurnal reptiles may be recorded in one area. For example, I have seen 10 of these 12 species at the Pisgah Crater, San Bernardino County, California. This area is a low lava flow with rocky habitat for *Sauromalus*, pockets of sand for *Uma* and *Dipsosaurus*, and adjacent creosotebush habitat where *Urosaurus* is common. Only *Crotaphytus collaris* and *Sceloporus magister* were not seen, but they may occur in the area.

In the present study, the reptiles species which were numerically most abundant did not constitute the largest component of the biomass. Thus, the energetic importance of each species would have been misunderstood if the weight data had

not been analyzed. Among the lizards, three species (*Cnemidophorus*, *Callisaurus*, and *Uta*) were present on all sites. All are insectivorous but differ in body size and feeding strategies (Tinkle 1967; Pianka 1970; Parker 1972; Tanner and Krogh 1975). The other lizards are different in size and food habits: *Phrynosoma platyrhinos* is a medium-sized specialist on ants; *Crotaphytus wislizenii* is a large-bodied predator on lizards and large insects; *Sceloporus magister* is a heavy-bodied insectivore; and *Dipsosaurus dorsalis* is a large-sized herbivore. All seven of these lizards are morphologically distinct and belong to different genera. Each species plays a characteristic ecological role which overlaps little with other species. The importance of each species in the community can be better assessed by using information about biomass and habits in addition to numbers of individuals.

My data show that the desert tortoise (*Gopherus agassizii*) is a major component of the creosote-shrub community in the Mojave Desert. Due to its large size and local relative abundance, *Gopherus* contributes a significant proportion of the biomass and energy turnover in this ecosystem. It is an important herbivore in these arid-land habitats.

A transect 1.6 km long and about 7–8 m wide was employed by Pianka (1965) to assess lizard populations. This sampling area traverses a diversity of microhabitats as soil, topography, vegetation, and other factors change with distance. For example, a linear transect in most bajadas will include sandy soils in washes, whereas interfluvial areas are composed of grus, rocky soil, or desert pavement. Upper reaches of bajadas are usually rocky, grading through gravelly conditions into alkaline flats at lower elevations. Thus, transects across or down a bajada may display different diurnal reptile communities.

Site-specific studies such as those of Turner et al. (1969a, 1969b, 1970) provide valuable population data on desert lizards, as intended, yet are generally inadequate to determine changes among several communities without an investment of great time. The removal method appears to be a useful compromise between these two approaches. The method encompasses a discrete plot of workable size (2 ha or more) in a relatively short time. Reptiles present can be related to different habitat variables such as vegetative structure and soils, which are needed to

better elucidate the niche requirements of arid-land reptiles under various environmental regimes.

Much remains to be learned about the structure, variation, and composition of reptile communities in arid lands. Future studies should question the relations between species diversity, abundance, and biomass, and how these population features relate to habitat conditions. Generally acceptable and standardized techniques would enable valid comparisons of data collected by different workers and predictions of the effects of perturbations on these ecosystems.

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TROPICAL HERPETOFAUNA

The Herpetofauna of Forest Litter Plots from Cameroon, Africa

by

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Abstract

Systematic samples of African forest litter herpetofaunas were made in Cameroon, Africa. Total species and taxonomic composition are compared between the African faunas and faunas from similar tropical forests of Asia and Central America. Data compared include total species and the taxonomic makeup of the samples.

Of special interest are the African samples that were taken in a forest established on a white-sand soil. This type of system is generally considered to be less productive than tropical forests growing on other types of soils; in Cameroon, the number of species was less than in Borneo or Costa Rica, but the number of individuals was about half of that found in Costa Rica and about six times that of Borneo.

In November–December 1975, the first quantitative herpetological collections from African wet forests, including systematic censuses of forest litter plots, were made in southwestern Cameroon, West Africa. This report compares these samples with similar studies in Borneo, Costa Rica, and Panama (Scott 1976).

The majority of the African samples was taken from a forest representing a well-defined subset of wet tropical forests—those growing on white-sand soils. These soils are found in many areas including parts of Borneo, Java, Malaya, Guyana, Suriname, Brazil, the Congo basin, and others. Janzen (1974) reviewed the known ecology of white-sand forests and hypothesized that they have a distinctive set of characteristics, chief of which are low fertility, relatively few tree species, well-protected tree leaves with an evergreen habit, slow recovery from disturbance, and low animal densities. The collections reported here enable us to test the latter generality.

Description of the Area

Collections were made at two sites in the

Douala-Edéa Game Reserve which lies south of the Sanaga River near its mouth (Fig. 1). The first site was near a field station on the eastern shore of Lac Tisongo and the second at Lombé, a field camp about 5 km southwest of the southern tip of the same lake. The whole area is lowland, probably not more than 30 m elevation. McKey et al. (1978) described the soils and details of the biochemistry of the trees.

The terrain at the Lac Tisongo site consists of a low hill that slopes gently down to the lake shore. The litter samples were taken on flat sites on the hill. The soil is a loamy sand with excellent drainage. The evergreen forest is largely undisturbed except by trappers and hunters. It is rather low in stature (emergents to 40 m) compared with Costa Rican forests receiving an equivalent amount of rainfall, and lianas and epiphytes are less abundant. Collecting was done within 2 km of the station.

The Lombé site is a flat plain shallowly dissected with small streams. Swampy areas are common, and even on higher ground shallow puddles persist after a heavy rain. The soil is sand with little or no clay and appears to conform well to the tropical white-sand forests de-

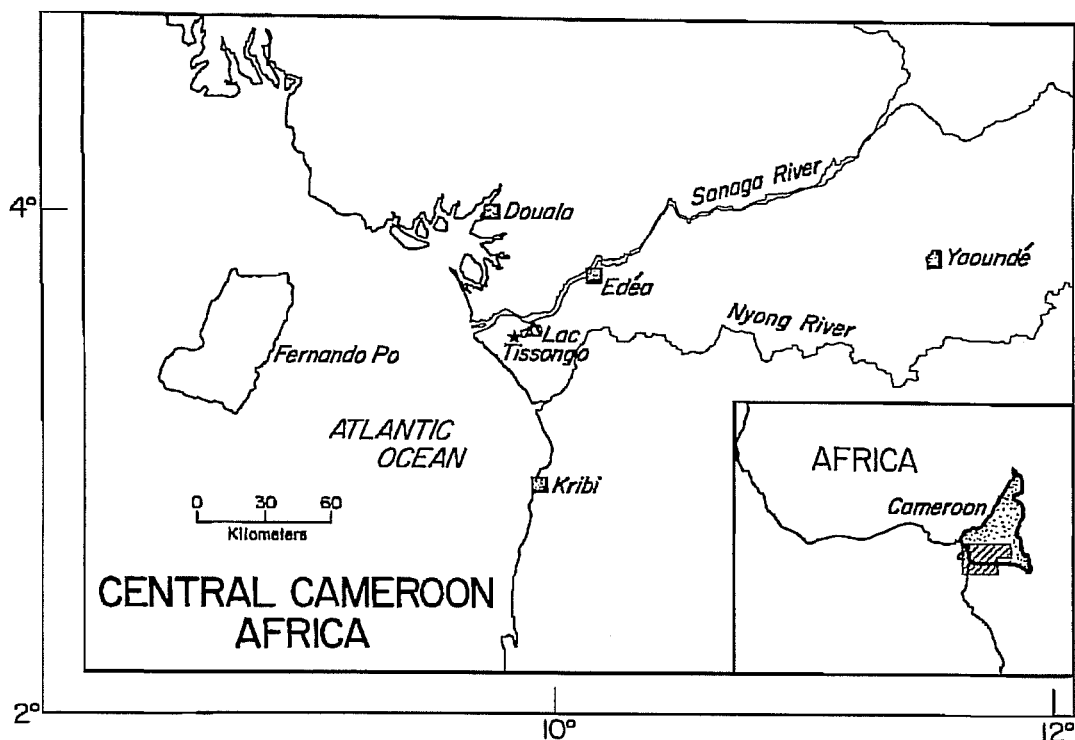


Fig. 1. Central Cameroon, Africa, showing location of study sites. The triangle is the Lac Tisongo camp, the star is Lombé.

scribed by Janzen (1974). The forest is well developed and only slightly shorter than at Lac Tisongo, but lianas are even rarer. There is only one palm; understory species are scarce. The litter samples were taken from a well-drained upland site, and all collections were made within 2 km of camp.

Rainfall in the two areas is about 4 m annually; an average of about 3 months receives less than 100 mm of rain (Suchel 1972). The samples were taken during the early part of the dry season.

Litter depth, measured at five points in each plot, averaged 2.6 cm at Lac Tisongo and 1.8 cm at Lombé. The litter was similar in depth and structure to that in Costa Rican lowland forests except that it was tightly bound together by fungal hyphae. Litter was thicker in the area of windfalls and under the emergent tree *Lophira*, which is one of the few synchronously deciduous trees in the forest (D. McKey, personal communication).

The forests on the two sites contain relatively few tree species in comparison with tropical for-

ests on more fertile soils (D. McKey, personal communication). Mammals were moderately common and included several species of monkeys and prosimians, chimpanzees, pangolins, bush pigs, several civets, mongooses, porcupines, waterbucks, two species of duikers, tree hyraxes, and elephants.

Methods

During late November and early December 1975, 15 square 58-m² plots were randomly located on the forest floor and cleared of litter. Five were at Lac Tisongo and 10 at Lombé. All frogs seen were tabulated and captured if possible. For further details of the methods used, see Lloyd et al. (1968) and Scott (1976). The results of these samples are compared with similar samples reported from La Selva and Osa, Costa Rica (Scott 1976); Sarawak, Borneo (Lloyd et al. 1968); and Barro Colorado Island, Panama (Heatwole and Sexton 1966; Myers and Rand 1969).

General collections were made in April (4 days, early wet season), November (18 days),

and December (6 days, early dry season) 1975. A variety of techniques were employed during a total of about 66 man-hours. These collections serve as the basis for estimating the total number of species present. Two species, a cobra (*Naja*) and a monitor (*Varanus*), were seen and tabulated but not collected.

Results and Discussion

Comparison between Lac Tissoongo and Lombé

Little difference existed between the two sets of African litter plots, especially in species composition (Table 1). The Lac Tissoongo samples yielded fewer animals per plot ($\bar{x} = 3.8$) than the Lombé plots ($\bar{x} = 6.3$). The difference was not statistically significant (Mann-Whitney U test; $P > 0.10$), but Lac Tissoongo may have lower densities. The samples are small, and half of the total Lombé plots each produced more animals than any one of the Lac Tissoongo samples. The difference in the number of animals may be a result of topography. In Costa Rica, slope samples regularly contained fewer animals (Scott 1976), probably because of the drier and more seasonal conditions on the well-drained upland soils. The Tissoongo samples were taken in hilly terrain whereas the Lombé plots were in flatland forest.

The data from the two African sites are lumped for the regional comparisons that follow. Table 2 is a list of 38 species collected from the African sites. I have indicated those that I consider to be regular litter inhabitants.

Animal Densities

The African litter plots are compared with samples taken from other lowland tropical areas with similar climates and vegetations (Table 3). Animal densities are 55–65% of those found in the lowlands of Costa Rica and Panama and six times the densities in Borneo. There were no lizards or snakes in the African plot samples.

African frog densities are surprisingly high considering the fact that two-thirds of the samples were taken from a white-sand forest. Theoretically, these forests are growing in a nutrient-poor environment that severely limits tree

Table 1. Occurrence of frogs in 15 Cameroonian forest litter plots. Samples taken in November and December 1975.

Species	Lac Tissoongo (5 plots)	Lombé (10 plots)	Totals (15 plots)
Bufonidae			
<i>Nectophryne batesi</i>	1	—	1
<i>N. afra</i>	3	3	6
<i>Bufo gracilipes</i>	1	—	1
Ranidae			
<i>Arthroleptis adelphus</i>	6	22	28
<i>A. sylvaticus</i>	6	24	30
<i>A. variabilis</i>	—	3	3
<i>Hylarana albolabris</i>	1	4	5
<i>Phrynobatrachus cornutus</i>	—	4	4
Escaped frogs	1	3	4
Totals	19	63	82
Individuals/100 m ²	6.5	10.8	9.4
Number of Species	6	6	8

growth rates and other primary production (Janzen 1974). Therefore, the trees hold individual leaves much longer and protect them with toxins and digestion-reducing compounds (McKey et al. 1978). When the leaves fall, they decompose very slowly because of the presence of these substances. To the litter community dependent on leaf fall for the great majority of its energy, this means that fewer leaves are decomposed and nutrients are released slowly. The Lombé forest had many of the characteristics of the white-sand system (McKey et al. 1978): white-sand subsoil, clear blackwater lakes and rivers (presumably from dissolved humic acids), a lack of synchronous or heavy leaf fall (except for *Lophira*), very few epiphytes and lianas, few mosquitoes, stunted crops, sparse second growth, few tree species, and low understory insect densities (D. McKey, personal communication). On the other hand, the streams contained a moderate number of fish, and mammals and birds were reasonably common in the forest. Evidently Lombé does not represent as extreme development of the white-sand forest as was studied by Janzen and Inger in Borneo (Janzen 1974). Possibly the African litter frogs have adopted certain of the adaptive strategies used by the trees. If that were true, we would expect them to be long-lived, unusually toxic, and to produce few young. Thus, the standing crop

Table 2. Reptiles and amphibians collected and observed near Lac Tisongo, Cameroon, Africa.

Species	Lac		
	Litter species	Tisongo camp	Lombé
Amphibia			
Bufonidae			
<i>Bufo camerunensis</i>	X	X	—
<i>B. gracilipes</i>	X	X	X
<i>Nectophryne afra</i>	X	X	X
<i>N. batesi</i>	X	X	X
Ranidae			
<i>Hylarana albolabris</i>	X	X	X
<i>H. sp. nov.</i>	—	—	X
<i>Phrynobatrachus</i>			
<i>auritus</i>	X	X	X
<i>P. cornutus</i>	X	—	X
<i>Ptychadena</i>			
<i>aequiplicata</i>	X	—	X
<i>Petropedates newtoni</i>	X	—	X
<i>Conraua crassipes</i>	—	—	X
<i>Arthroleptis adelphus</i>	X	X	X
<i>A. sylvaticus</i>	X	X	X
<i>A. taeniatus</i>	X	—	X
<i>A. variabilis</i>	X	X	X
Hyperoliidae			
<i>Leptopelis aubryi</i>	—	X	—
<i>L. brevirostris</i>	—	X	X
<i>L. boulengeri</i>	—	—	X
<i>L. millsoni</i>	—	—	X
Reptilia			
Lacertilia			
Gekkonidae			
<i>Hemidactylus</i>			
<i>echinus</i>	—	X	X
<i>H. fasciatus</i>	—	X	X
<i>H. muriceus</i>	X	X	X
<i>Lygodactylus</i>			
<i>conraua</i>	—	—	X
<i>L. fischeri</i>	—	—	X
Scincidae			
<i>Mabuya affinis</i>	X	X	X
<i>M. polytropis</i>	X	—	X
<i>Panaspis breviceps</i>	X	—	X
<i>P. reichenowi</i>	—	X	—
Chamaeleontidae			
<i>Chamaeleo cristatus</i>	—	X	—
<i>C. quilensis</i>	—	X	X
Lacertidae			
<i>Holaspis guentheri</i>	—	—	X
Varanidae			
<i>Varanus sp.</i>	X	—	X

Table 2. Continued

Species	Lac		
	Litter species	Tisongo camp	Lombé
Serpentes^a			
Boidae			
<i>Python sebae</i>		—	X
Elapidae			
<i>Naja sp.</i>		—	X
Colubridae			
<i>Boiga pulverulenta</i>		—	X
<i>Dipsadoboa unicolor</i>		—	X
<i>Philothamnus semi-</i>			
<i>variegatus</i>		—	X
<i>Thelotornis kirtlandi</i>		X	—

^aSnakes were not considered to be part of the litter herpetofauna.

would be relatively high but population turnover may be reduced compared with areas containing more soil nutrients.

The lack of lizards and snakes in the African litter samples reflects a real difference between them and the forests studied in Borneo and Central America. The only analog of stem-perching litter-feeding lizards of the American genera *Anolis* and *Norops* was a scarce diurnal gecko, *Hemidactylus muriceus*, and *Panaspis breviceps* was the only African lizard similar to the American litter microteids or the diurnal gecko, *Lepidoblepharis*. Mongooses (*Herpestes auripunctatus*) were seen several times during the study, and perhaps Janzen's (1976) hypothesis that African reptile faunas are suppressed by small omnivorous predators applies here.

The only common terrestrial lizards were quick, heliothermic skinks, ecologically similar to New World *Ameiva*. They were found near houses or in windfall clearings that contained tangles of dead and living vegetation. Arboreal lizards were somewhat more common and widespread. Adult *Varanus* were seen twice. They are probably semi-aquatic and resistant to mongoose predation.

During 66 collecting hours in Cameroon, I took a *Thelotornis* and a *Python* and saw a *Naja*. Three other snakes were brought to me: a *Boiga*, a *Dipsadoboa*, and a *Philothamnus*. Herpetologists on Barro Colorado Island, Panama, took 11 species during 91 h of wet-season

Table 3. Comparison of litter plot samples from American, Asian, and African tropical lowlands. Bornean data from Lloyd et al. (1968), Costa Rican from Scott (1976), and Panamanian from Heatwole and Sexton (1966) and Myers and Rand (1969).

Region	Area within plots (m ²)	Individuals per 100 m ²	No. of species taken in litter plots	No. of regular litter species
Sarawak (Borneo)	23,342	1.5	41	38
La Selva and Osa (Costa Rica)	2,266	17.1	23, 23	34, 35
Barro Colorado Island (Panama)	512	14.6	15	27
Lac Tisongo and Lombé (Cameroon)	872	9.4	8	~18

collecting, and 6 species during 54 h in the dry season (Myers and Rand 1969). In Costa Rica, collectors usually take at least one to three snakes per day in lowland wet forest. All of the Cameroonian snakes I collected were arboreal or well protected by venom or size, even though mongooses can probably take them under some circumstances (Struhsaker and McKey 1975). These observations of relatively low snake densities and the species composition of my Cameroonian collections are similar to Janzen's (1976) reptile census data and support his suggestion that predation is an important regulator of African reptile population densities.

Species Number

The number of species in the African litter samples is only about half of that found in equivalent-sized samples from the other tropical areas (Table 3). Curves plotting the number of species vs. the number of individuals in the different tropics show a steady rise to 17 to 21 species in Borneo and Central America, whereas the African samples plateau at 8 species (Fig. 2). If a plateau is considered to be the collection of 20 or more specimens without adding a new species, the first La Selva, Borneo, and Osa plateaus represent respectively 50, 55, and 60% of the total number of litter species. If eight species represent 55% of the African fauna, we would expect 15 regular litter species. This is somewhat low since I have tabulated 18 (Table 2), but our knowledge of the habits of the African species is scanty, and some of the "litter" species may not belong in that category.

A depression in the number of species of frogs and lizards in a Bornean white-sand forest has been reported by Inger (in Janzen 1974). A

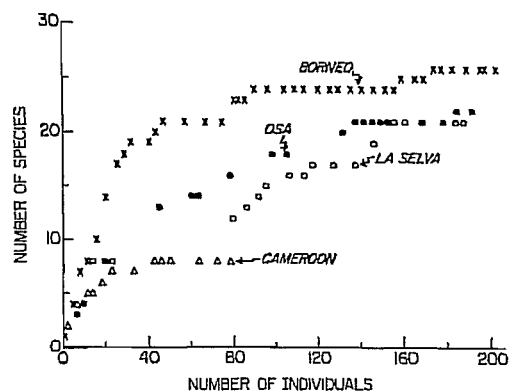


Fig. 2. Number of species collected in first 78 or more specimens of litter plot reptiles and amphibians in Cameroon; La Selva and Osa, Costa Rica (Scott 1976); and Borneo (Lloyd et al. 1968).

white-sand site had 37 species (litter and non-litter species) whereas two non-sand forests yielded 66 and 84 species, respectively. Janzen interpreted this to mean that the white-sand forest was a relatively harsh environment that was inhabited by a small number of well-adapted species.

The African general collections yielded about the same proportion of lizard species (32%) as appear in Costa Rican litter faunas (26% La Selva, 31% Osa). In Borneo, 45% of the fauna was lizards. Heyer and Bervan (1973) and Scott (1976) suggest that the American frog genus *Eleutherodactylus* serves as an ecological replacement for small lizards because of its capability to undergo development independently of free water. In Cameroon, the genus *Arthroleptis* has a similar capability and were the commonest frogs in the litter samples.

Although the African litter samples yielded relatively few species, the total forest habitat seems to hold a substantial number. Comparison of the number of species vs. collecting hours for Cameroon and Barro Colorado Island, Panama, shows very similar curves (Fig. 3). Duellman and Myers collected 43 species of reptiles and amphibians in 91 man-hours on Barro Colorado Island in the wet season (Myers and Rand 1969), and I took or saw 35 species in 66 h. Barro Colorado Island contains about 100 species of reptiles and amphibians. It is very likely that Lombé and Lac Tissoongo harbor nearly as many, since no frogs were breeding during the collecting periods, and frog choruses are favorite sources of diverse samples for herpetologists.

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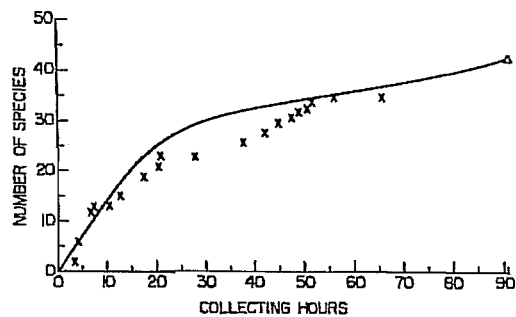


Fig. 3. Cumulative number of reptile and amphibian species collected per collecting hour in Cameroon (X) and Panama (curve and Δ; Myers and Rand 1969).

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SANDY SOIL HERPETOFAUNAS

Herpetofaunal Survey of the Sinai Peninsula (1967-77), with Emphasis on the Saharan Sand Community¹

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Abstract

The local interest in biogeography and ecology, and the paucity of data from areas surrounding Israel, led to intensive herpetological collecting in Sinai in 1956-57 and since 1967. Material in the Hebrew University of Jerusalem and in Tel-Aviv University together exceeds 1,000 specimens, comprising one species of toad, *Bufo viridis*, four species of marine turtles, and 50 species of terrestrial reptiles. Of these, one was first reported from Sinai in 1957, nine in 1973, and two, *Caretta caretta* and *Rhynchocalamus melanocephalus*, herein. Twenty-two species which occur in contiguous areas of Israel or Egypt or both, or have been reported from Sinai in the literature, were absent in the collected material. The sand dunes of northern Sinai are inhabited by a "community" of 10 psammophile reptile species of Saharan or Saharo-Arabian distribution. Each represents a different family or a genus of distinctive body size. Resource partitioning between related forms is sometimes indicated. Several other species which are not strict psammophiles (mainly snakes) also occur in these dunes.

The land bordering the eastern Mediterranean Sea is of great ecological-biogeographical interest (Furth 1975). Wallace's (1876) concept of a vast circum-mediterranean Mediterranean Region of heterogeneous or transitional nature is no longer acceptable to local biogeographers. Instead, four major ecological-biogeographic regions are now distinguished in the area (Bodenheimer 1956; Zohary 1970, 1973), and this division appears applicable to the herpetofauna (Bodenheimer 1937; Werner 1971). These regions are the Mediterranean (*sensu stricto*) scrubland and woodland (annual precipitation usually above 300 mm), the Saharo-Arabian desert (annual precipitation usually much under

150 mm), the intervening Irano-Turanian steppe (intermediate and irregular rainfall), and the hot and dry Sudanian (Ethiopian) penetration area (Haas and Werner 1969:367-368, Fig. 13; Zohary 1970:map c).

In Israel the Irano-Turanian is only a narrow belt between the Mediterranean in the North and the desert in the South. Consequently there is an abrupt transition (or very steep gradient) between the two floristic regions. The fauna of the Irano-Turanian is poorly developed so that the sudden break between desert and non-desert enhances the interest of various ecological problems to local biologists.

However, before 1967 Israeli herpetologists were restricted to studying reptiles and their distributions within confined and unnatural spatial boundaries. These boundaries could not be transcended nor could much information be obtained regarding reptile populations in adjacent areas. Thus, when access to the Sinai peninsula was gained, briefly in the winter of 1956-57 and again since the summer of 1967, Israeli

¹Dedicated to the memory of Hermann Zinner, who lived to see but the budding fruit of his love for desert reptiles.

²This report was prepared while the author was a visiting associate professor at the Department of Anatomy, University of Chicago, Chicago, Illinois.

herpetologists (in common with other scientists) endeavored to research the area thoroughly.

The landscapes of the Sinai Peninsula consist of sand dunes in the north, hills of sedimentary limestone and alluvial flats in the center, and steep mountains of ancient sandstone and magmatic rocks in the south. Biogeographically, the northern and central parts are Saharo-Arabian, the southern high mountains (above 1,500 m) are Irano-Turanian, and the southeastern and southwestern slopes of these mountains are Sudanian (Bodenheimer 1937; Zohary 1970; Haim and Tchernov 1974).

Previously the herpetofauna of Sinai was poorly known because collecting in the area had always been difficult, especially in terms of administration, logistics, and personal safety. The main relevant publications are those by Heyden (1827), Hart (1891), Barbour (1914), Bodenheimer (1937), Haas (1943), Schmidt and Marx (1956), and Hoofien (1965); some attention has also been given to Sinai in works on the Egyptian herpetofauna by Anderson (1898), Flower (1933), Loveridge (1947), and Marx (1968). Marx (1968) reported on material mainly from two circumscribed areas in Sinai, the El 'Arish area in the northern dunes and the Gebel Katherina range in the southern mountains. Two of these contributions contain formal checklists of the herpetofauna of Sinai: Flower (1933:738-740) who comments (p. 737), "Sinai is the richest part of Egypt herpetologically; it is by no means completely explored, and yet 42 species are known," and Schmidt and Marx (1956:37) who list 50 discrete taxa.

Some results of the recent extensive collecting were summarized by Hoofien (1972), Werner (1973), and Zinner (1974). An updated reptile checklist for Israel and Sinai is currently being compiled (Hoofien and Werner, unpublished data), employing manually prepared locality-record maps (Werner 1977). Moreover, for the more common squamate species, a detailed computerized study of geographical variation of meristic and mensural characters (for the area Turkey-Sinai, inclusive) is under way (Kosswig et al. 1976; Kosswig and Werner, unpublished data). The purpose of the present paper is (1) to give a brief interim report of the herpetological survey of Sinai, indicating the material and the main results, in terms of species found and species expected but not found, and (2) to point out certain noteworthy aspects of the herpetofaunal component of the Saharan sand dune community of northern Sinai. Reference is made

only to the principal papers dealing with the distribution and identification of the various species. It is impossible to review here the literature on the biology and ecological physiology of the species, although the literature is mostly based on adjacent Egyptian or Negev populations and hence relevant.

Materials and Methods

This report relies on the herpetological material from Sinai in the zoological museums of the Hebrew University of Jerusalem (HUJ; over 700 specimens) and of Tel-Aviv University (TAU; over 300 specimens). It has been impractical to examine the material which may be available in minor collections throughout Israel. Much of the material used had been collected in the course of a survey of the distribution of rodents throughout Sinai (Haim 1969). Other material had been added by numerous travelers, often on field trips with extraneous objectives, or incidentally to service in the Army. Most of these trips followed popular routes to selected localities. Very few trips (essentially, mine) were specially planned to collect reptiles along transects from which data were lacking.

Specimens in the collections were identified by standard keys (Barash and Hoofien 1956; Marx 1968) or more specific literature when necessary. The material was listed on species sheets with the locality data, which were then entered on species maps by topographical grid references (Werner 1977). Where original locality records lacked grid references, the latter were reconstructed from Survey of Israel, Ministry of Labour, maps or consultation with the collectors.

Locality record maps for 48 species were presented elsewhere (Werner 1973) and are not repeated here, although some additional records have been obtained. Perusal of these maps shows a general lack of data from two areas: the alluvial flats (around Qal'at en Nakhal) in central Sinai, an uninteresting landscape largely shunned by field trips, and the Suez Canal area where travel commonly was risky or forbidden.

Taxonomic names used in this report are those currently accepted by Israeli herpetologists (Hoofien 1972; Werner 1973).

Results and Comments

Species Found

Of the species known to inhabit the Sinai (Table 1), the only amphibian represented is *Bufo viridis* and that only from the northeast corner of Sinai. Here, as in the Negev of Israel, this Palearctic toad reaches the southern (desertic) limit of its distribution (Werner 1948; Wahrman 1970). Specific searches and inquiries for other frogs, especially in the larger oases, remained fruitless.

Of the Chelonía, *Testudo kleinmanni* occurs in the northern dunes, and *Caretta caretta*. *Chelonía mydas*. *Eretmochelys imbricata*, and *Dermochelys coriacea* are represented from the Sinaitic Mediterranean and Red Sea shores.

Of the Sauria, the Gekkonidae are represented by eight or nine species: *Cyrtodactylus scaber*, *Hemidactylus flaviviridis*, *H. turcicus turcicus*, *Ptyodactylus hasselquistii guttatus*, *P. h. cf. hasselquistii*, *Stenodactylus petrii*, *S. sthenodactylus sthenodactylus*, *Tarentola mauritanica mauritanica*, and *Tropiocolotes steudneri*. The two *Ptyodactylus* forms, currently regarded as subspecies (Werner 1965), may well be distinct species. *P. h. guttatus* occurs in northern Sinai and in the south on mountains, whereas *P. h. cf. hasselquistii* lives inside the wadis and canyons of the south. The two are sympatric in the Abu Zanima area on the Gulf of Suez and their vocalizations differ markedly (Frankenberg 1974; Werner et al. 1978). By studying the diel activity cycle in an aktograph, Frankenberg (1976, 1977, 1978, 1979) found that *P. h. hasselquistii* is more nocturnal than *P. h. guttatus*. The taxonomy of the group is presently under review (Y. L. Werner, unpublished data).

Agamidae.—Six species: *Agama pallida pallida*, *A. savignii*, *A. sinaita*, *A. stellio brachydactyla*, *A. stellio* subsp., *Uromastix aegyptius* and *U. ornatus*. The nomenclature for *Agama pallida* has been discussed elsewhere (Werner 1971:228). Despite the work of Duan (1967), the taxonomy of *Agama stellio* in Sinai remains uncertain. *A. s. brachydactyla* occurs in the north but southern specimens are different, as has also been suggested by Flower (1933:775).

Chamaeleonidae.—Specimens available from the northern dunes are juveniles, apparently assignable to *Chamaeleo chamaeleon musae*; some may be intergrades between *C. c. musae*

and *C. c. recticrista* Boettger, 1880, of Mediterranean Israel (Hoofien 1964).

Scincidae.—Five species: *Ablepharus kitaibelii*, *Chalcides ocellatus*, *Eumeces schneideri schneideri*, *Scincus scincus*, and *Sphenops sepsoides*. Part of the distribution of *Sphenops sepsoides* was presented earlier (Werner 1968) on the basis of the 1956–57 Sinai expeditions.

Lacertidae.—Six species: *Acanthodactylus baskianus asper*, *A. scutellatus scutellatus*, *Eremias brevisrostris*, *E. guttulata*, *E. olivieri*, and *E. rubropunctata*. Some authors (e.g., Marx 1956, 1968) do not distinguish between *Eremias guttulata* and *olivieri* but they are indeed distinct in morphology (Haas 1951a; Barash and Hoofien 1956) and habitat: *guttulata* occurs on various soils including rocks but not on sand; *olivieri* occurs on sand and sand mixtures; in some places the two occur together but suspected hybrids are rare. The occurrence of *Eremias brevisrostris* in southernmost Sinai was first reported by Hoofien (1957) on the basis of specimens from the 1956–57 expeditions.

Varanidae.—There is only one specimen, *Varanus griseus griseus* (TAU), probably because the species is both protected and difficult to capture.

Among the Ophidia, the Typhlopidae are represented by *Typhlops vermicularis* and the Leptotyphlopidae by *Leptotyphlops macrorhynchus* (= *L. phillipsi* Barbour 1914, Hahn 1978), the occurrence of which has recently been reconfirmed in the Santa Catherina area.

Colubridae.—Eight "aglyphous" species: *Coluber jugularis asianus*, a single specimen from Gebel Hillal in northeastern Sinai (TAU; the species-group has recently been revised by H. Zinner in an unpublished dissertation), *C. ravergeri nummifer* (from Wadi Feiran only), *C. r. rhodorhachis*, *C. rogersi*, *Eirensis coronelloides*, *Lytorhynchus diadema*, *Rhynchocalamus melanocephalus*, and *Spalerosophis diadema cliffordi*.

Five "opisthoglyphous" species: *Malpolon mollensis*, *Psammophis aegyptius*, *P. schokari*, *Telescopus dhara*, and *T. hoogstraali*. According to Zinner (1977) *T. hoogstraali* is a subspecies of *T. fallax* (Fleischmann, 1831).

Elapidae.—Only *Walterinnesia aegyptia*.

Viperidae.—Five species, *sensu lato*: *Atractaspis engaddensis*, *Cerastes cerastes*, both horned and unhorned specimens; *C. vipera*; *Echis colorata*, and *Pseudocerastes fieldi*. Sochurek (1974) has claimed priority for a new subspecies,

Table 1. Amphibian and reptile species from the Sinai. One asterisk indicates species first reported by Werner (1973); two asterisks indicate those found since then; three asterisks indicate species probably present but never recorded.

AMPHIBIA	Lacertidae
Salientia	<i>Acanthodactylus boskianus asper</i> (Audouin, 1829)
Bufonidae	<i>A. scutellatus scutellatus</i> (Audouin, 1829)
<i>Bufo viridis</i> Laurentius, 1768	<i>Eremias brevirostris</i> (Blanford, 1874)
REPTILIA	<i>E. guttulata</i> (Lichtenstein, 1823)
Chelonia	<i>E. olivieri</i> (Audouin, 1829)*
Testudinidae	<i>E. rubropunctata</i> (Lichtenstein, 1823)
<i>Testudo kleinmanni</i> Lortet, 1883	Varanidae
Cheloniidae	<i>Varanus griseus griseus</i> (Daudin, 1803)
<i>Caretta caretta</i> (Linnaeus, 1758)**	Ophidia
<i>Chelonia mydas</i> (Linnaeus, 1758)*	Typhlopidae
<i>Eretmochelys imbricata</i> (Linnaeus, 1758)*	<i>Typhlops vermicularis</i> Merrem, 1820
<i>Dermochelys coriacea</i> (Linnaeus, 1766)*	Leptotyphlopidae
Sauria	<i>Leptotyphlops macrorhynchus</i> (Jan, 1864)
Gekkonidae	Boidae
<i>Cyrtodactylus scaber</i> (von Heyden, 1827)	<i>Eryx jaculus</i> (Linnaeus, 1758)***
<i>Hemidactylus flaviviridis</i> Rueppell, 1835	Colubridae
<i>H. turcicus turcicus</i> (Linnaeus, 1758)	<i>Coluber jugularis asianus</i> Boettger, 1880*
<i>Ptyodactylus hasselquistii guttatus</i> von Heyden, 1827	<i>C. ravergeri nummifer</i> Reuss, 1834
<i>P. h. cf. hasselquistii</i> (Donndorff, 1798)	<i>C. r. rhodorhachis</i> (Jan, 1865)
<i>Stenodactylus petrii</i> Anderson, 1896	<i>C. rogersi</i> (Anderson, 1893)
<i>S. sthenodactylus sthenodactylus</i> (Lichtenstein, 1823)	<i>Eirenis coronelloides</i> (Jan, 1862)
<i>Tarentola mauritanica mauritanica</i> (Linnaeus, 1758)	<i>Lytorhynchus diadema</i> (Duméril and Bibron, 1854)
<i>Tropiocolotes steudneri</i> (Peter, 1869)	<i>Macroprotodon cucullatus</i> (Geoffroy St. Hilaire, 1827)***
Agamidae	<i>Malpolon moileensis</i> (Reuss, 1834)*
<i>Agama pallida pallida</i> Reuss, 1833	<i>M. monspessulanus</i> (Hermann, 1804)***
<i>A. savignii</i> Duméril and Bibron, 1837	<i>Psammodromus aegyptius</i> Marx, 1958*
<i>A. sinaita</i> von Heyden, 1827	<i>P. schokari</i> (Forskål, 1775)
<i>A. stellio brachydactyla</i> Haas, 1951*	<i>Rhynchocalamus melanocephalus</i> (Jan, 1862)**
<i>A. stellio</i> (Linnaeus, 1758) subspecies	<i>Spalerosophis diadema cliffordii</i> (Schlegel, 1837)
<i>Uromastix aegyptius</i> (Forskål, 1775)	<i>Telescopus dhara</i> (Forskål, 1775)
<i>U. ornatus</i> von Heyden, 1827	<i>T. hongstrauli</i> Schmidt and Marx, 1956
Chamaeleonidae	Elapidae
<i>Chamaeleo chamaeleon musae</i> (Steindachner, 1900)	<i>Walterinnesia aegyptia</i> Lataste, 1887*
Scincidae	Viperidae
<i>Ablepharus kitaibelii</i> Bibron and Bory, 1833	<i>Atractaspis engaddensis</i> Haas, 1950
<i>Chalcides ocellatus ocellatus</i> (Forskål, 1775)	<i>Cerastes cerastes</i> (Linnaeus, 1758)
<i>Eumeces schneideri schneideri</i> (Daudin, 1802)	<i>C. vipera</i> (Linnaeus, 1758)
<i>Scincus scincus</i> (Linnaeus, 1758)	<i>Echis colorata</i> Cuenther, 1878
<i>Sphenops sepsoides</i> (Audouin, 1829)	<i>Pseudocerastes fieldi</i> Schmidt, 1930

Cerastes cerastes karlhariti (southwestern Sinai), without differentiating it from the typical form.

Comparison of this herpetofaunal list with lists of adjacent Israel (Cisjordan) (Haas 1951b, 1952; Werner 1966), Jordan (Transjordan) (Haas 1943, 1951b; Werner 1971), and Africa (Egypt) (Anderson 1898; Flower 1933; Marx

1968) shows that the herpetofauna of Sinai, as represented by the recent collections, is not exactly identical with any of the other areas (Fig. 1). On the other hand, none of the species is strictly endemic to Sinai, although *Uromastix ornatus* extends only slightly into southern Israel.

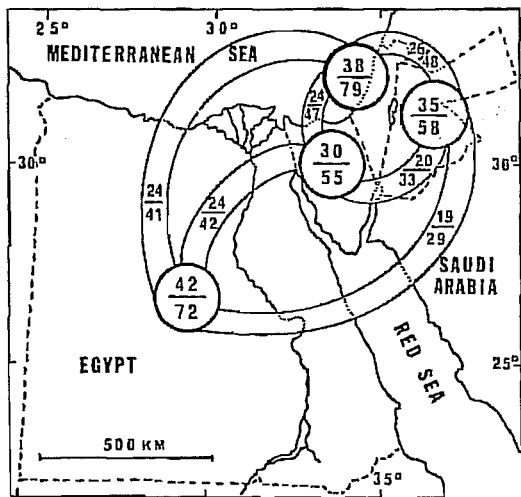


Fig. 1. Relations of the reptilian fauna of Sinai to those of surrounding Israel, Jordan, and Egypt. Broken lines demarcate survey areas; figures in circles represent the number of lizard species (numerator) and the total number of land and freshwater reptile species (denominator) in each. Figures in connecting arcs represent the numbers of species in the two categories that are common to two areas. The data for lizards are given because these are probably more complete than those for snakes, and to facilitate comparison with Anderson's (1968:367) similar diagram for southwestern Asia.

Species Not Found

Three species of snakes (*Eryx jaculus*, *Macroprotodon cucullatus*, and *Malpolon monspessulanus*) known from both southern Israel and Egypt are not represented in my material (nor reported in the literature) from the intervening Sinai but very probably occur in that area.

On the other hand, three reptiles (*Trionyx triunguis*, *Mabuia vittata*, and *Natrix tessellata*) known from both Israel and Egypt and not represented in the collections may actually be absent from Sinai due to the scarcity or absence of suitable habitats. *Natrix tessellata* occurs in Yemen as well but probably as a relict (Leviton 1977). Its single literature record from Sinai has been discussed by Hoofien (1965). Absence of suitable habitats may likewise apply to *Mabuia quinquetaeniata*, which occurs in Egypt as far east as the west bank of the Suez Canal, or the Suez Canal may act as a barrier for this and other species.

Several other reptiles not represented in my material have been reported at one time or another from Sinai in the literature (details in Flower 1933; Hoofien 1965; Marx 1968): *Pelomedusa subrufa* (apparently an error); *Hemidactylus sinaitus* (recent material from Sinai does not fully conform to the description); *Tarentola annularis* (no explanation suggested); *Tropicolotes nattereri* (likely to be confirmed on reexamination of the material); *T. tripolitanus* (Marx's 1968 record was based on a half-dried specimen from El 'Arish [U.S. National Museum of Natural History no. 133490] which I identify as a juvenile *Stenodactylus petrii*); *Agama mutabilis* (the specimens on which this is based differ from North African ones and are assignable to *A. pallida*); *Uromastix acanthinurus* (no explanation); *Acanthodactylus pardalis* (erroneously based on an *A. boskianus*, H. Marx, personal communication, a piquant situation since the species abounds in both Egypt and the Negev of Israel but its preferred loess soil does not occur in Sinai); *A. cantor* (erroneous); *Eremias mucronata* (probably erroneous); *Lastia longicaudata* (either introduced or erroneous); *Ophisops elegans* (probably correct for restricted habitats); *Coluber sinai* (no explanation); *Eirenis coronella* (refers to *E. coroneloides*, J. H. Hoofien, personal communication). Additionally, a record of *Coluber elegantissimus* (Negumi 1949) awaits verification.

The total herpetofauna of Sinai may include at least 60 species.

The Saharan Psammophile Community

Of all the reptiles of Sinai, those inhabiting the northern sand dunes constitute the most clearly defined community, or community fraction, in that many of them are strict psammophiles not occurring on adjacent soils (Table 2). The morphological adaptations of such species to life in and on sand have been discussed by Buxton (1923), Mosauer (1932, 1936), and many others. In terms of ecological biogeography, the core of this community comprises 10 truly psammophilous species of essentially Saharan, or Saharo-Arabian, distribution. Together with many other psammophilous organisms, they support the characterization of these dunes, which are indicated on maps presented by Werner (1968) and Haim and Tchernov (1974), as an extension of the Sahara (*sensu lato*).

Table 2. Amphibians and reptiles of the northern Sinai sand dunes.

Psammophile Species	
	<i>Testudo kleinmanni</i>
	<i>Stenodactylus petrii</i>
	<i>Agama savignii</i>
	<i>Scincus scincus</i>
	<i>Sphenops sepsoides</i>
	<i>Acanthodactylus scutellatus</i>
	<i>Eremias olivieri</i>
	<i>Varanus griseus</i>
	<i>Lytorhynchus diadema</i>
	<i>Cerastes vipera</i>
Euryoecious Species	
	<i>Stenodactylus sthenodactylus</i>
	<i>Coluber rogersi</i>
	<i>Spalerosophis diadema</i>
	<i>Psammophis schokari</i>
	<i>Walterinnesia aegyptia</i>
Species of Particular Microhabitats	
	<i>Bufo viridis</i>
	<i>Hemidactylus turcicus</i>
	<i>Tarentola mauritanica</i>
	<i>Chamaeleo chamaeleon</i>

Interestingly, each of the species represents a different family, or at least a genus of distinct body size; no two members of any one genus are included. In most instances, however, vicarious congeners occur on the adjacent non-sandy soils, and often other psammophilous congeners occur on disjunct sand areas elsewhere in Sinai or Israel. Thus the Testudinidae are represented in the Saharan north Sinai dunes by *Testudo kleinmanni*, which is replaced by *T. graeca* in the more northern coastal plain dunes (and other soils) of Israel. Among the Sauria, in the family Gekkonidae, *Stenodactylus petrii* is replaced in the Wadi Araba dunes by *S. doriae*, and on other light soils by *S. sthenodactylus*. This latter species also occurs in the dunes, especially north of the range of *S. petrii*, but also sympatrically with it (Haas 1956; Werner and Broza 1969). In the Agamidae, *Agama savignii* is replaced on adjoining loess soils, and on sands elsewhere, by *A. pallida*. The two skinks, *Scincus scincus* and *Sphenops sepsoides*, coexist. *Scincus scincus* is limited to these dunes, whereas *S. sepsoides* also occurs in sand elsewhere. Where the latter does not occur, *Chalcides ocellatus*, normally inhabiting other soils, occurs in the sand. I found these two species together only at the northern extreme of the range of *S. sepsoides*, near Caesarea

on the Mediterranean coast. The lacertid, *Acanthodactylus scutellatus*, is replaced by *A. boskianus* on adjacent light soils and on unconnected Sinai sands, and by *A. schreiberi* on northern Israel's coastal dunes (Werner 1952); *Eremias olivieri* is replaced on adjacent non-sand by *E. guttulata*, although the two may coexist on sandy loess. *Varanus griseus* is the only varanid of the area. *Lytorhynchus diadema* is the only sand-limited colubrid in the area. *Cerastes vipera* is the sand viper of the northern dunes, and is replaced on inland sands by *C. cerastes* or *Pseudocerastes fieldi* and on other soils by *Echis colorata*. Excellent descriptions and illustrations of almost all of these species were provided by Anderson (1898).

Population density has not been estimated for any of the species. From observations and collecting, *Acanthodactylus scutellatus* is by far the most common cursorial diurnal reptile on the dunes, although its density may well be matched by that of the subterranean *Sphenops sepsoides*, and perhaps by the nocturnal *Stenodactylus petrii*. *Eremias olivieri* and *Scincus scincus* appear to be much rarer.

In some instances there are indications of how competition between related forms may be reduced. Of the two sympatric *Stenodactylus* species, *petrii* has much larger eyes than *sthenodactylus*, implying that the former is more strictly nocturnal (Werner 1969). Aktograph studies of Frankenberg (1977:16-17) also indicate that *petrii* may be more nocturnal than *sthenodactylus*, at least in spring. Moreover, individuals of *S. sthenodactylus* have been observed in the field in autumn and winter out in the open in daytime (E. Frankenberg 1977:79, personal communication). Among the scincids, there is some evidence that *Scincus* is diurnal, whereas the somewhat smaller *Sphenops* is nocturnal. Among the lacertids, the adult *Eremias* is only as large as a juvenile *Acanthodactylus*. Of the lizards, only *Agama savignii* is known to eat plant material in addition to insects. Among the snakes, both *Lytorhynchus* and *Cerastes vipera* prey on lizards, but the much broader head and the venomous character of the latter presumably facilitate a much wider scope of food items.

In addition to these arenicolous species, a number of more euryoecious species, particularly snakes, are also found in these sands. *Stenodactylus sthenodactylus*, *Coluber rogersi*,

Spalerosophis diadema, and *Psammophis schokari* are probably most frequently encountered but others, including *Walterinnesia aegyptia*, also occur.

A special example is *Chamaeleo chamaeleon*, which lives in bushes and grass clumps in the dunes, but it is hardly a psammophile in terms of adaptation to locomotion on sand. The toad, *Bufo viridis*, and the climbing geckos, *Hemidactylus turcicus* and *Tarentola mauritanica*, occur in suitable mesic niches within the dunes.

Conclusions

This survey of Sinai carried out in 1956-57 and 1967-77 greatly increased our knowledge of the herpetofauna of this once relatively poorly known corner of the Near East. The herpetofauna of the Sinai Peninsula comprises at least 50 and possibly some 60 terrestrial reptile species, 4 marine turtles, and 1 toad. None of the species is completely endemic to the territory of Sinai. Each occurs in at least a small portion of at least one of the adjacent territories: the Negev desert of Israel, the Transjordanian desert, and the Eastern Desert of Egypt. Certain additional species, known from either or both Egypt and Israel, may yet be discovered in Sinai.

The literature records of several species from Sinai may be erroneous, and those of some others may yet be confirmed. The sand dunes of northern Sinai support a community of 10 Saharan psammophile reptile species, each representing a separate family or a genus of distinctive body size. Resource partitioning is apparent between some species. Most of these psammophiles are replaced by vicarious species both on disjunct sand areas and on adjacent non-sand soils. Several additional euryoecious species, mostly snakes, also occur in the same dunes.

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The Herpetological Components of Florida Sandhill and Sand Pine Scrub Associations

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Abstract

Investigations of the herpetofauna of the peninsular Florida sandhills and sand pine scrub revealed a diverse complex composed of a minority of xeric-adapted species combined with an array of wide-ranging and aquatic species that can be found in many Florida habitats. The xeric-adapted species required sand for burrowing or sand-swimming. The tortoise (*Gopherus*) digs burrows that serve as shelter for several other species; the wide-ranging generalist species, however, require none of the specialized conditions of the sandhills and scrub. Sand scrub, especially early successional stages, contains 22 species of reptiles and amphibians, which is more than in any other of a wide range of peninsular Florida habitats. Apparently the herpetofauna is responding to the dry, well-drained soil and patches of sand free from roots rather than to any aspect of the vegetation. The sand-swimming species (*Eumeces egregius*, *Tantilla relicta*, and *Neoseps regnoldsii*) depend on periodic disturbance (e.g., fire and clear-cutting) to remove the matted understory and pine canopy. The widespread distribution of these forms attests to the continuous presence, throughout history, of a mix of successional stages in both the sandhills and sand pine scrub.

The sandhill and scrub pine plant associations are characteristic and well defined elements of the Florida environment. Although vegetatively distinct, they are closely related physically and geographically (Fig. 1) and have very similar herpetofaunas. Autecological studies of sandhill and scrub species are available (Telford 1959; Jackson 1972; Smith, this volume), but, in contrast to extensive literature on the vegetation, previous research has not dealt with the community of animals living in these plant associations. The sandhills and sand pine scrubs, along with xeric hammocks, form the principal habitats in Florida for a distinctive herpetofauna based on xeric-adapted forms.

We initiated studies (Florida Fish and Game Commission 1976) in these habitats in the spring of 1975 using the methods detailed elsewhere (Campbell and Christman, this volume). In 1976

we substantially increased our efforts in the various subtypes of sandhill and scrub in the Ocala National Forest in central Florida to determine the distribution and relative abundance of amphibian and reptile species in the various successional stages of sandhills and scrub.

Characterization of the Habitats

Sandhill Association

The sandhill association and its successional relations to other Florida plant associations have received considerable attention over the years (Laessle 1958), and there is general agreement on the physical and phytogeographic characteristics of the sandhills. References to the reptiles and amphibians occurring in the sandhills generally use the designators "High Pine" (Carr 1940) or "Longleaf-pine/Turkey-oak" (Laessle 1942). Similar habitats, differing only slightly in

¹Deceased: Died at Gainesville, Florida, on 10 December 1981.

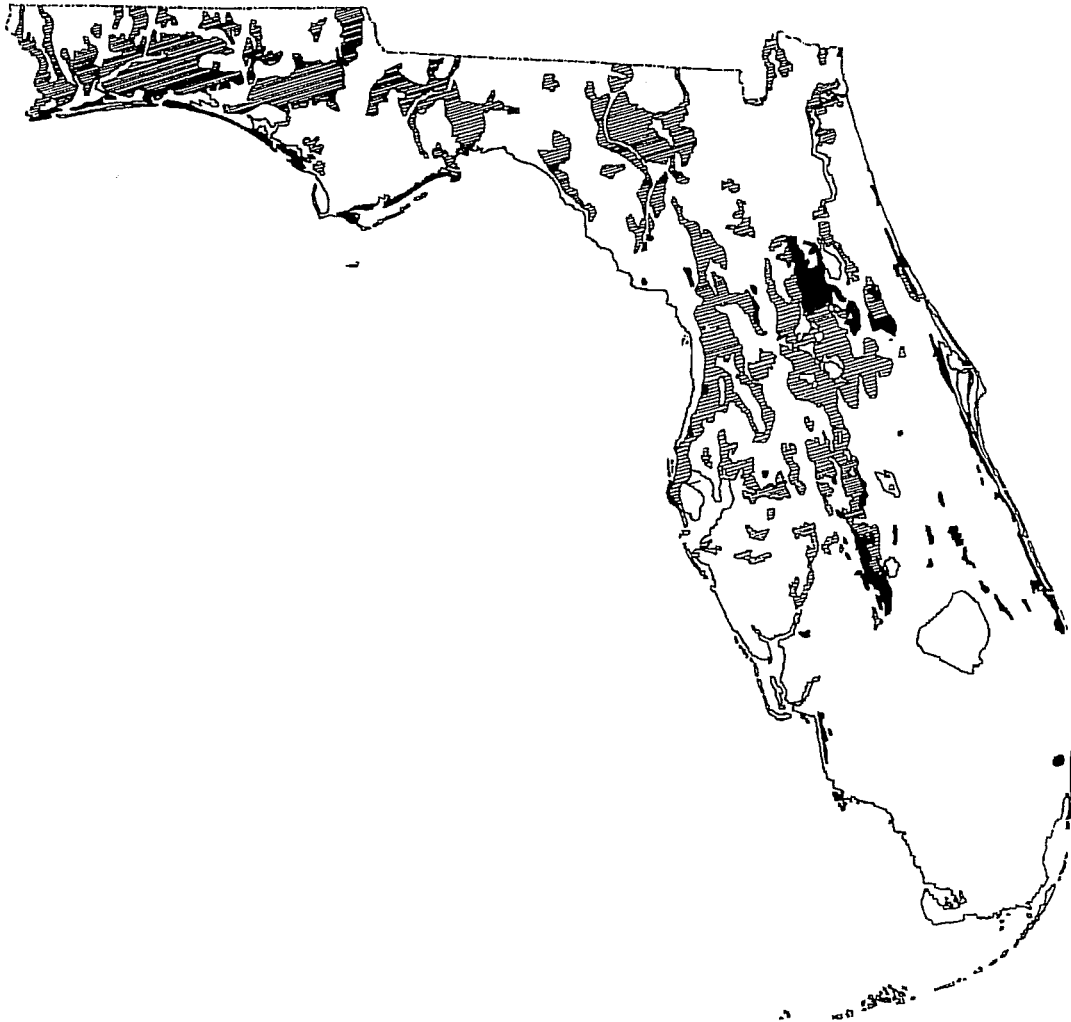


Fig. 1. Distribution of sandhills (hatched) and sand pine scrub (black) in Florida (Davis 1967).

their plant species, are found in scattered areas having suitable soils throughout the southern United States (Laessle 1958; Bozeman 1971), but the sandhills of the Florida peninsula support a herpetological community that is distinct from the sandhills of the Florida panhandle and other areas of the southeast. The following analysis will deal specifically with the peninsular sandhills.

Most sandhills in peninsular Florida occur on well-drained, sandy soils of the Lakeland series as defined by Gammon et al. (1953) and Laessle (1958). The physical characteristics of these soils and their similarity to the soils supporting sand pine scrub and xeric hammock, as well as the

relative frequency of fire in these associations, are considered to be the factors determining which animals use these habitats. Sandhills are generally restricted to soils of slightly higher clay and silt content than those supporting the scrub association (Laessle 1958).

The sandhill association exists in two basic forms in peninsular Florida: the "typical" longleaf pine (*Pinus palustris*)/turkey oak (*Quercus laevis*) association, and the turkey oak sandhills. The typical phase is a three-tiered habitat with widely-spaced longleaf pines forming the upper level, an understory of scattered turkey oak (bluejack oak, *Q. incana*, may replace turkey oak on lower soils of the Blanton series), and a

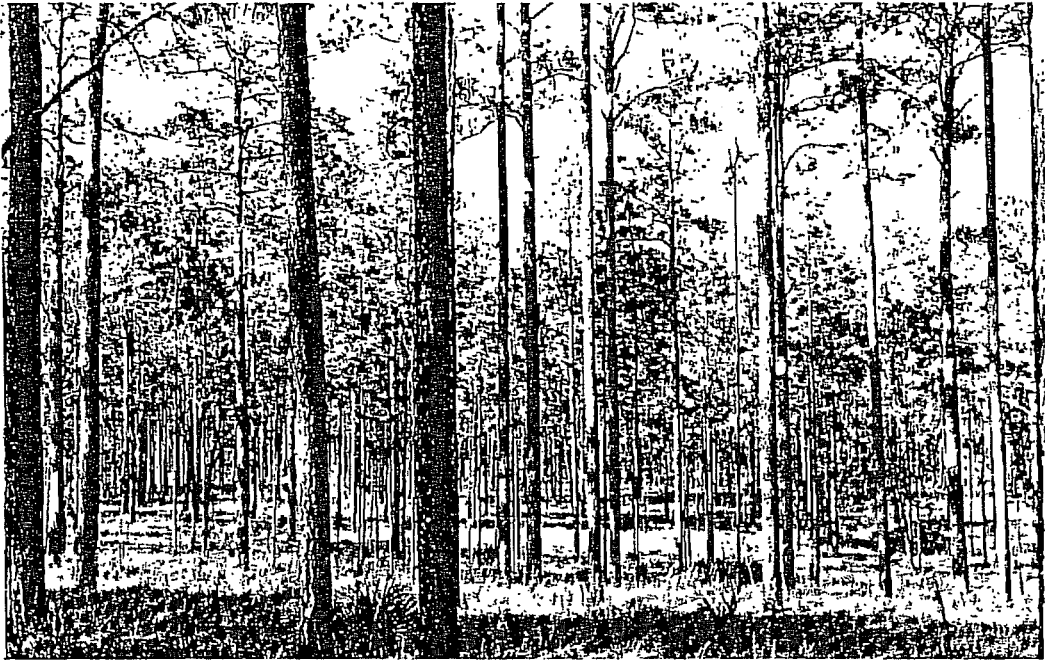


Fig. 2. Typical phase of the longleaf pine-turkey oak sandhill habitat in the Ocala National Forest, Florida.

ground cover dominated by wire grass (*Aristida stricta* and *Sporobolus gracilis*, Fig. 2). Fire is frequent in this habitat, perhaps the most widespread of the fire subclimax associations in Florida. The dominant plant species are fire resistant.

Where the longleaf pines are removed, the turkey oak increases in height, forming the canopy layer at 8–10 m, and the ground cover becomes less dense with frequent and extensive areas of bare sand interspersed with drifted piles of oak leaves and scattered vegetation (Fig. 3). Fire is also a frequent phenomenon in the turkey oak sandhill and often results in extensive areas of open sand and occasional damage to the oaks.

The turkey oak sandhill is by far the predominant phase of sandhill habitat remaining in peninsular Florida; lumbering demands on the longleaf pine long ago eliminated it over extensive areas of sandhill habitat. Today the Riverside Island area of the Ocala National Forest (Fig. 2) is perhaps the largest and least disturbed stand of the "typical" longleaf pine-dominated sandhill habitat remaining in the southeastern United States (Florida Game and Fresh Water Fish Commission 1976).

Sand Pine Scrub Association

The sand pine scrub association occurs throughout Florida in isolated patches, often associated with or adjacent to sandhills (Fig. 1). The soils that support scrub habitat are of the St. Lucie series and are essentially loose, unconsolidated sands, similar to but coarser and looser than those which support sandhills. There is never standing or running water in scrub habitats, as even the heaviest rains percolate immediately into the loose sand. Mulvania (1931: 528) referred to these soils as "... a bed of silica, to which the term soil is but remotely applicable." The Florida scrub has been called the ecological equivalent of the California chaparral (Laessle 1967).

Botanists have been intrigued with scrub since its description early in the last century (Vignoles 1823). Perhaps no plant community in Florida has stimulated more interest or more printed words (e.g., Vignoles 1823; Nash 1895; Whitney 1898; Harper 1914, 1921; Mulvania 1931; Webber 1935; Kurz 1942; Laessle 1942, 1958, 1967; Miller 1950; Cooper et al. 1959; Veno 1976).

Characteristic scrub tree species include the

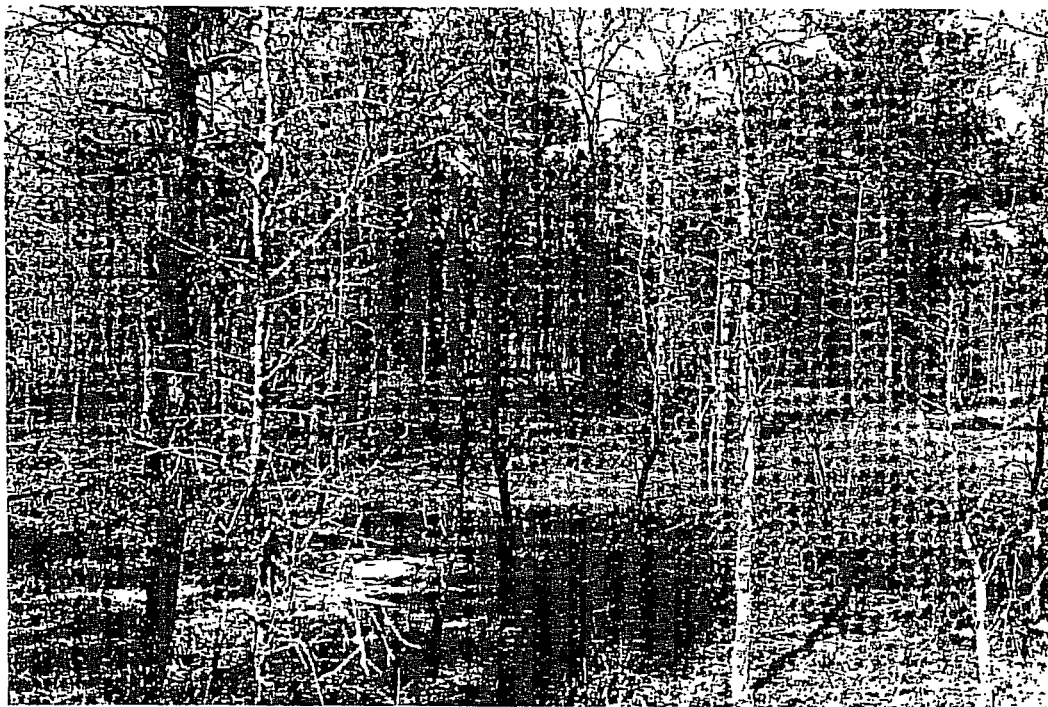


Fig. 3. Turkey oak phase of the longleaf pine-turkey oak sandhill habitat in the Ocala National Forest, Florida.

sand pine (*Pinus clausa*), various evergreen oaks (*Quercus virginiana*, *Q. myrtifolia*, and *Q. chapmani*), and lyonia (*Lyonia ferruginea*). Scrubs can be divided into two major types: those with sand pine trees and those without. The latter are sometimes referred to as rosemary scrubs. It is not always clear why some scrubs lack sand pines. Where the pines have died of old age in the absence of fire, scrubs sometimes persist for many years (Laessle 1967). Other evergreen oak scrubs appear never to have had sand pines. The Florida scrub jay (*Aphelocoma coerulescens*), the sand skink (*Neoseps reynoldsi*), and the Florida scrub lizard (*Sceloporus woodi*) are largely restricted to the evergreen oak scrub without sand pines and to those scrubs with young sand pines.

Scrubs rarely burn but, when they do, the fire usually crowns, killing the sand pines. Under the extreme heat of a crowning fire, the sand pine seeds are released from the serotinous cones. More often than not, scrubs are adjacent to sandhill communities which burn frequently.

Many authors have noted the tendency of ground fire in the sandhills to stop abruptly at the sandhill-scrub ecotone (e.g., Webber 1935; Laessle 1967). The dominant sandhill tree, longleaf pine, is well adapted to survive frequent ground fires which are readily kindled by the wire grass and deciduous oak leaves which accumulate rapidly. On the other hand, the evergreen oaks of the scrub provide little fuel for ground fires. Thus Webber (1935) referred to the scrub as a "fire fighting association." If fire is excluded from the scrub, the sand pines eventually die of old age and the habitat may ultimately succeed to hardwood (oak, magnolia) hammock (Veno 1976). When a scrub burns, however, the sand pines are killed, seeds are released, and the cycle begins again. At first there are extensive areas of open sand, but the vegetation gradually fills in to form an almost impenetrable tangle composed of a matted ground cover, a dense evergreen shrub layer, and a full pine canopy characteristic of a mature scrub.

Table 1. Categories of reptile and amphibian species occurring in sandhills and scrubs in peninsular Florida.

Characteristic	Occasional
Xeric adapted	<i>Hyla cinerea</i>
<i>Eumeces egregius</i>	<i>H. crucifer</i>
<i>Neoseps reynoldsi</i>	<i>H. squirella</i>
<i>Sceloporus woodi</i>	<i>Pseudacris ornata</i>
<i>Masticophis flagellum</i>	<i>Ophisaurus attenuatus</i>
<i>Stilosoma extenuatum</i>	<i>O. ventralis</i>
<i>Tantilla relicta</i>	<i>Sceloporus undulatus</i>
<i>Cnemidophorus sexlineatus</i>	<i>Drymarchon corais</i>
Wide-ranging	<i>Elaphe guttata</i>
<i>Scaphiopus holbrooki</i>	<i>E. obsoleta</i>
<i>Gastrophryne carolinensis</i>	<i>Heterodon simus</i>
<i>Bufo quercicus</i>	<i>Storeria occipitomaculata</i>
<i>B. terrestris</i>	<i>Thamnophis sirtalis</i>
<i>Rhineura floridana</i>	<i>Crotalus adamanteus</i>
<i>Anolis carolinensis</i>	Associated with
<i>Eumeces inexpectatus</i>	Aquatic Habitats
<i>Scincella laterale</i>	<i>Acris gryllus</i>
<i>Cemphora coccinea</i>	<i>Rana catesbeiana</i>
<i>Coluber constrictor</i>	<i>R. grylio</i>
<i>Micrurus fulvius</i>	<i>R. sphenacephala</i>
Associated with	<i>Ambystoma talpoideum</i>
Tortoise Burrows	<i>A. tigrinum</i>
<i>Rana areolata</i>	<i>Notophthalmus perstriatus</i>
<i>Gopherus polyphemus</i>	<i>N. viridescens</i>
<i>Pituophis melanoleucus</i>	<i>Pseudobranchius striatus</i>
Frequent	<i>Siren intermedia</i>
<i>Hyla femoralis</i>	<i>S. lacertina</i>
<i>H. gratiosa</i>	<i>Chrysemys floridana</i>
<i>Ophisaurus compressus</i>	<i>C. nelsoni</i>
<i>Diadophis punctatus</i>	<i>Deirochelys reticularia</i>
<i>Heterodon platyrhinos</i>	<i>Kinosternon bauri</i>
<i>Lampropeltis triangulum</i>	<i>K. subrubrum</i>
<i>Opheodrys aestivus</i>	<i>Sternotherus odoratus</i>
<i>Sistrurus miliarius</i>	<i>Nerodia fasciata</i>
	<i>Seminatrix pygaea</i>
	<i>Thamnophis sauritus</i>
	<i>Agkistrodon piscivorus</i>

Results

General

Several distinct groups of amphibian and reptile species occur in the sandhills and scrub (Table 1): those that can be considered to be highly adapted to a xeric, sandy habitat (i.e., reaching maximum population levels or found only there); those that occur throughout a wide habitat spectrum; those species associated with burrows of tortoise (*Gopherus polyphemus*); and those species that occur in or near aquatic

habitats surrounded by sandhills, scrub, or any other terrestrial habitat.

All of the xeric-adapted species except the Florida scrub lizard require loose, well-drained sand for burrowing or sand-swimming. *Gopherus* and associated species are also dependent on sandy soils for burrows. These species are restricted to sandhill, scrub, and xeric hammock habitats, although *Tantilla relicta* may rarely occur in more mesic habitats. *Gopherus polyphemus* deserves special mention as a focal species in providing burrow refuges for a wide variety of other species including *Rana areolata*

and *Pituophis melanoleucus*, which are essentially restricted to this microhabitat in peninsular Florida. *Drymarchon corais*, generally considered a characteristic gopher tortoise burrow inhabitant, is not so restricted in peninsular Florida and may actually reach greater population levels in certain more mesic hardwood habitats. Its close relation to gopher tortoise burrows and xeric habitats is encountered primarily at its range margins in Georgia and Alabama; in peninsular Florida the burrows are more commonly used by *Pituophis* and a variety of other snake species.

The aquatic species occurring in the sandhills and scrub may reach high population levels around appropriate habitat but are best considered fortuitous additions to the species list. The greatest number of species occurring in the sandhill and scrub habitats are ecological generalists which find suitable conditions in a wide variety of habitats. Unfortunately, we know too little of absolute population densities of amphibian and reptile species to be able to judge relative habitat quality for most species and thus cannot rank the value of sandhills and scrub to these generalist species. On inspection of Table 1, however, it is clear that the generalists are all species which require none of the specialized physical or vegetative conditions of the sandhill and scrub associations.

Scrub Species Diversity

The community of herpetologists in Florida has long been familiar with the scrub endemics (*Neoseps reynoldsi* and *Sceloporus woodi*), but when our data showed that scrubs had the highest amphibian and reptile species richness of 11 terrestrial habitat types sampled (Table 2), we decided to look more closely at what Carr (1940:8) called, "... undoubtedly the most rigorous habitat in Florida. . . ."

We list 43 nonaquatic species of amphibians and reptiles as known to occur either characteristically, frequently, or occasionally in Florida scrubs and sandhills (Table 1). Two of these, *Neoseps reynoldsi* and *Sceloporus woodi*, are primarily restricted to scrub habitat. Others (e.g., *Eumeces egregius*, *Eumeces inexpectatus*, *Cemophora coccinea*, *Tantilla relicta*) may reach their greatest abundance in some successional stage of the scrub habitat. Still others oc-

Table 2. Results of the herpetological trapping program by habitat type, Cross Florida Barge Canal Wildlife Restudy. *Eleutherodactylus planirostris*, an exotic species, has been omitted.

Habitat type	Total number of species	Number of individuals/array/day
River swamp	3	0.05
Slash pine flatwoods	7	0.07
Longleaf pine flatwoods	16	0.13
Pond pine flatwoods	6	0.17
Hydric hammock	17	0.23
Mesic hammock	12	0.21
Xeric hammock	10	0.15
Longleaf pine sandhills	13	0.22
Deciduous oak sandhills	16	0.11
Evergreen oak scrub	21	0.16
Sand pine scrub (mature)	19	0.14

cur in scrub only near its ecotone with sandhills or along roads through the scrub (e.g., *Copherus polyphemus* and its symbionts).

The reptiles that inhabit the scrub proper fall into two categories: those that "swim" beneath the sand surface (Mosauer 1932) and those that run on the surface of the sand. Even lizards such as *Anolis carolinensis* and *Sceloporus woodi* spend much time on the surface, as pit-fall records indicate. *Neoseps reynoldsi*, *Eumeces egregius*, and *Tantilla relicta* are the principal sand swimmers, although other small species are frequently encountered beneath the sand surface (e.g., *Scincella laterale*, *Lampropeltis triangulum*, *Heterodon platyrhinos*). Smith (this volume) investigated the details of the niches of the three principal sand-swimming species.

Amphibians are poorly represented in the scrub. *Notophthalmus perstriatus* efts occasionally inhabit the scrub. Only the most xeric-adapted anurans will be found regularly in true scrub. Turtles are essentially lacking, although *Kinosternon bauri* may occasionally wander through scrubs, and *Copherus polyphemus* will occur near roads and ecotones where the soil will sustain burrow construction. Snake and lizard diversity is high.

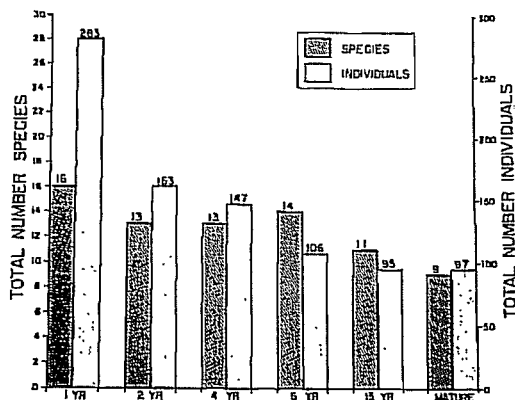


Fig. 4. Total numbers of species and individuals of reptiles and amphibians collected in various ages of sand pine scrub in the Ocala National Forest, Florida.

Scrub and Sandhill Succession

Our ongoing trapping program in the Ocala National Forest was designed to determine if there are any differences in the terrestrial herpetofauna between different-aged stands of sand pine scrub and between the facies of the sandhill association. We installed two standardized trapping arrays in turkey oak and longleaf pine sandhills and in each of six various-aged stands of even-aged sand pine. During the first 10 months of this sampling, we collected 891 specimens of 22 species in the scrub traps (Fig. 4). These results suggest strongly that some species are more abundant in the younger stands of scrub while others are more abundant in the more mature scrubs. No species is confined to the more mature scrubs, although several species collected in the younger stands have not been taken in the mature scrub. Of 22 species collected, only *Anolis carolinensis*, *Scincella laterale*, and possibly *Eumeces inexpectatus* are more abundant in the older scrubs. On the other hand, at least six species occur more frequently in the younger scrubs. Notable among these are *Scaphiopus holbrooki*, *Cnemidophorus sexlineatus*, *Sceloporus woodi*, and *Tantilla relicta*. The 1-year, 2-year and 4-year-old sites have thus far produced 593 specimens of 20 species, whereas the 6-year, 15-year, and mature sites have yielded only 298 specimens of 16 species. A similar pattern characterized the turkey oak and longleaf pine sandhills. We believe that addi-

tional collecting will not appreciably change this trend; that is, it appears that species richness and animal abundance decrease as the pines mature or, to be more specific, as the ground cover increases.

Discussion

It appears to us that the amphibian and reptile fauna occurring in the sandhills and scrub is not actually responding to a particular plant association, but rather to the physical characteristics of the habitat. Where these physical characteristics are met in other plant associations (e.g., xeric hammock), many of the same vertebrate species occur. Thus the scrub lizard and the sand skink are really adapted to habitats that are dry, well-drained, and offer patches of open sand, free from rooted vegetation. We can think of no amphibian or reptile species in Florida that has a distribution restricted to a single plant association. Actually, we argue that the plant species occurring in a given habitat are responding to many of the same environmental factors as the animals. Perhaps wildlife habitats should be classified according to the significant physical characteristics to which both the plants and the animals are adapted rather than by plant associations. The present system can lead to misleading judgments, and we offer a single example: the Florida gopher tortoise is known from several "habitats" (i.e., plant associations): longleaf pine sandhills, deciduous oak sandhills, evergreen oak scrub, sand pine scrub, xeric hammock, dry flatwoods, and a host of ruderal situations. Does this mean that the gopher tortoise is a highly-adaptable, ubiquitous species? It does not. Gophers are essentially restricted to habitats with well-drained, sandy soils, and an abundance of grasses and forbs, and ultimately, with maximal light intensity at ground level (Auffenberg and Franz 1980). These conditions can be met in a variety of places regardless of the specific plant species living there.

A comparison between longleaf pine and turkey oak sandhill may shed light on the evolution of the highly adapted sandhill and scrub reptile and amphibian species. Aside from the presence or absence of a pine canopy and the corresponding dwarfing or enlargement of the understory oaks, these facies of the association are strikingly different in the nature of the ground cover. The

longleaf pine-dominated sandhill usually supports a dense ground cover of wire grass and forbs, whereas the turkey oak-dominated facies is more open, often with extensive areas of bare sand, and it receives more intensive surface insolation. The reptiles characteristic of the sandhills are, as noted, species which burrow and highly specialized sand "swimmers." Species such as *Tantilla relicta*, *Eumeces egregius*, and *Neoseps reynoldsi*, which require loose sand for sand swimming, historically have encountered such conditions in the sandhills only in areas of disturbance, such as the burrow mounds of *Gopherus polyphemus* and *Geomys pinetis*, or the open areas resulting from fire, especially under a turkey oak canopy. In the longleaf pine/turkey oak association such conditions (minus man's imposition of road shoulders and other disturbances) are localized islands of loose sand protruding from a cover of wire grass. Similarly, the mat of roots and humus covering the sand in the mature sand pine scrub would require breaks to provide suitable conditions for these species.

Neoseps reynoldsi, *Eumeces egregius*, *Tantilla relicta*, and *Stilosoma extenuatum* are also more abundant in early successional stages of sand pine scrub than they are in the advanced stages with a full pine canopy, dense evergreen shrub layer, and matted ground cover. To provide conditions for the evolution of the endemic or characteristic species of the sandhills and scrub, there must have always been such disturbed areas where loose surface sand was available. Despite the contention that the central sandhills of Florida were historically blanketed by a sheet of longleaf pine/turkey oak (Laessle 1958), it would appear more probable that a mix of successional stages, both in sandhills and sand pine scrub, has always existed. Breaks in the typical or mature stages of both habitats could, and probably did, result from severe fires, tornado or hurricane blow-downs of the canopy trees, outbreaks of pine-bark beetles, or other natural disasters. These factors would have maintained a mix of habitats amply supplied with the open, loose sand conditions needed for the evolution of the unique herpetological components of the peninsular Florida sandhill and scrub associations. These species, especially *Neoseps reynoldsi*, *Tantilla relicta*, and to a lesser extent, *Eumeces egregius*, are thus cast as "weed" species, colonizers of a

patchy early successional or disturbed habitat type which occurs throughout the sandhill, sand pine scrub, and xeric hammock vegetative associations as a result of biological (*Gopherus*, etc.) or catastrophic (fire) factors.

Although most of the highly adapted scrub and sandhill fauna meet few or none of the biological requirements typically cited for colonizing species (see Baker and Stebbins 1965), they must be considered colonizers because of the short-lived nature of their required habitat. A population of sand skinks cannot persist to its maturity in a patch of sand pine scrub; they invade young scrubs opened by killing fires, scrubs without sand pine, and sandhills without wire grass and longleaf pines. Just how a species with a reproductive rate of only one or two young per female per year (Telford 1959) and such apparently poor vagility can do this is a question worth pursuing.

In our current study of the scrubs of the Ocala National Forest, we consistently trapped more species and more individuals in the younger sand pine scrubs. This suggests that there are either more animals in the younger stands or that those present are easier to trap. It is clear that the recently clear-cut scrub is more frequently used by "typical" scrub species; when we consider the natural history of scrub (i.e., fire ecology), this makes sense. It should come as no surprise that the scrub-adapted fauna is accustomed to survival in even-aged stands of sand pine. It thus appears that clear-cutting and even-age management of sand pine stands may mimic the natural situation of infrequent crown fire to which the scrub fauna is adapted.

The variables of a herpetological association or "community" in the scrub and sandhills habitat are difficult to define. Many of the most common species are broadly distributed and only fortuitously juxtaposed in the sandhills and scrub; the more specialized species occur only in restricted microhabitats. With only a few exceptions, the species list for these areas can be duplicated in various other habitat types in peninsular Florida. If we exclude aquatic habitats, the species list is virtually identical to that for xeric hammock.

It appears evident from these data that the concept of a herpetological association or "community" cannot be defined along plant association boundaries in the xeric habitats of peninsular Florida. The local distribution of species is

determined by a complex of physical and probability factors at least partially independent of the plant species of the area. The most heuristic approach is to view amphibian, reptile, and plant species as responding to a similar set of physical and biotic factors without assuming any interdependency between species. If the definition of a herpetological "community" is to be more than the fortuitous association of a group of individuals of a variety of species at a specific place and time, we must look beyond the plant association. In the xeric habitats of peninsular Florida, the particular plant associations appear less important than the presence or absence of areas of loose dry sand.

Acknowledgments

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Food Resource Partitioning of Fossorial Florida Reptiles

by

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Abstract

Tantilla relicta, *Eumeces egregius*, and *Neoseps reynoldsi* share the same habitat within the scrubs and sandhills of central Florida. Stomach analyses of specimens from several localities show considerable differences in their arthropod prey. *Tantilla relicta* inhabits surface litter and specializes on tenebrionid larvae. *Eumeces egregius* is a surficial skink which generalizes on blattids, crickets, and spiders. *Neoseps reynoldsi* possesses an anatomy specialized for subsurface "sand-swimming" and takes a variety of prey, including termites, tenebrionid larvae, spiders, and antlions. The food resource overlap of *Neoseps reynoldsi* with the other two species is apparently reduced by its adaptations to a subsurface microhabitat.

Tantilla relicta, *Eumeces egregius*, and *Neoseps reynoldsi* are fossorial, insectivorous squamates which occur sympatrically within the scrubs and sandhills of central Florida. The food habits of *T. relicta* and its relationship to the two lizard species in their common habitats are unknown.

The sand skink, *Neoseps reynoldsi*, has the wedge-shaped snout, counter-sunk jaw, and drastically reduced limbs of a highly specialized "sand-swimmer." Cooper (1953) and Myers and Telford (1965) provided the only published references to the sand skink's diet. *Eumeces egregius*, the mole skink, has a more generalized anatomy with typical limbs but also swims through the sand. Its food habits are reported in Hamilton and Pollack (1958) and Mount (1963). *Tantilla relicta*, the crowned snake, also possesses the wedge-shaped head and counter-sunk jaw which permit efficient sand-swimming. No published reference to the prey items of this species exists, but literature on the food of *T. coronata* (Hamilton and Pollack 1956) and *T. gracilis* (Force 1935) is available.

Methods and Materials

The Cross Florida Barge Canal Restudy (Flor-

ida Game and Fresh Water Fish Commission 1976) and a current study in the Ocala National Forest, Marion County, Florida, by the National Fish and Wildlife Laboratory provided the bulk of examined specimens. A few additional *N. reynoldsi* were also used.

Pitfalls and funnel traps in conjunction with drift fences (Campbell and Christman, this volume) constituted the primary collection technique. In the Ocala study, 20 arrays with four fences each were emplaced in July 1976 and checked weekly through December 1977. The 10 Ocala study sites, each with two arrays, included turkey oak (*Quercus laevis*) and longleaf pine (*Pinus palustris*) sandhills, evergreen oak scrub, and various ages of sand pine (*Pinus clausa*) scrub from clearcut to mature stand. The Barge Canal study traps involved from one to four arrays in each of the 11 following habitats: turkey oak and longleaf pine sandhills; evergreen oak and sand pine scrub; hydric, mesic, and xeric hammocks; longleaf pine, slash pine (*Pinus elliottii*), and pond pine (*Pinus serotina*) flatwoods; and mixed swamp. The trapping at the Canal site began in spring 1975, sampling periods were 1 to 2 weeks, and trapping was concluded in December 1975. All trap sites were in or adjacent to the Ocala National

Forest with the exception of a turkey oak sandhill located 24 km southwest of Ocala and 14 km east of Dunnellon. In addition to the arrays, more conventional field work supplied further material for examination. All specimens were frozen the day of capture for later preservation.

The scrubs and xeric hammock are upland habitats associated with an extensive paleodune field of infertile silicious sand with high internal drainage. The Ocala scrubs occur on whitish sands of the St. Lucie and Lakewood series (Laessle 1958). Vegetation includes sand pine, myrtle oak (*Quercus myrtifolia*), saw palmetto (*Serenoa repens*), rosemary (*Ceratiola ericoides*), and lichens (*Cladonia* spp.). As sand pine scrub matures, the shrubby understory and ground litter become more extensive. Campbell and Christman (this volume) describe sand pine scrub regeneration. If no regenerative mechanism occurs, the sand pines may decline due to senescence and the area may succeed to evergreen oak scrub or xeric hammock. Small oaks such as the myrtle oak dominate the evergreen oak scrub and open patches of sand develop between clumps of the oaks and rosemary bushes. A slightly moister soil probably gives rise to xeric hammock dominated by live oaks (*Quercus virginiana*).

The well-drained upland sandhills occur on yellow infertile sands of the Lakeland series. Longleaf pine, turkey oak, wild persimmon (*Diospyros virginiana*), live oak, and two wire grasses (*Aristida stricta* and *Sporobolus gracilis*) commonly occur in sandhills. When the pine trees are lumbered, turkey oak dominates the sandhill, herbaceous ground cover is reduced, and open patches of sand develop. These disturbed sandhills approach scrub conditions with a consequent reflection in their faunal assemblages (Campbell and Christman, this volume).

The mesophytic and hydrophytic sites are characterized by much poorer drainage than the scrubs and sandhills mentioned above and the data confirmed the virtual absence of the three species of squamates in these areas. For this reason, habitat descriptions are omitted here and the reader is referred to Snedaker and Lugo (1972).

In all, 219 *Tantilla relicta*, 164 *Eumeces egregius*, and 14 *Neoseps reynoldsi* were available for examination of stomachs. The Barge Canal study totals included six *T. relicta* and

two *N. reynoldsi* which were caught by hand. In addition, four *N. reynoldsi* from the Sebring area in Highlands County were examined.

The stomach and intestinal contents of all of the specimens were removed and placed in small vials containing 75% isopropyl alcohol. The contents of each vial were placed in a petri dish under a variable power (7-30X) dissecting scope, segregated and identified according to Chu (1949) and Borror and DeLong (1964). Only the number and frequency of different food items were recorded.

Results

A number of factors were analyzed for each species, including spatial and temporal activity or presence, adaptations, and food habits. Habitat and microhabitat preferences comprised the spatial component. Seasonal activity was plotted from July 1976 to December 1977 to determine any temporal differences between the three species.

Habitat Preference

Tantilla relicta was common in the longleaf pine and younger stands of sand pine scrub. Turkey oak sandhill, xeric hammock, and the drier evergreen oak scrub had moderate populations. Specimens were trapped rarely in the wetter evergreen oak scrub site. *Eumeces egregius* was taken commonly in the turkey oak sandhill, most younger sand pine scrubs, and evergreen oak scrub. The mature sand pine scrub, longleaf pine sandhill, and xeric hammock arrays trapped few or none, but occasional individuals were collected by hand from all of these habitats. *Neoseps reynoldsi* was trapped rarely and only in the Ocala turkey oak sandhill.

Annual Activity

Seasonal variation in numbers was plotted to determine any temporal activity differences in the three species (Figs. 1 to 3). The initial high values in Figs. 1 and 2 resulted from trapping a previously undisturbed population. Thereafter the values leveled off to a true reflection of activity. Peaks of activity occurred in the September-October and March periods, and inactivity

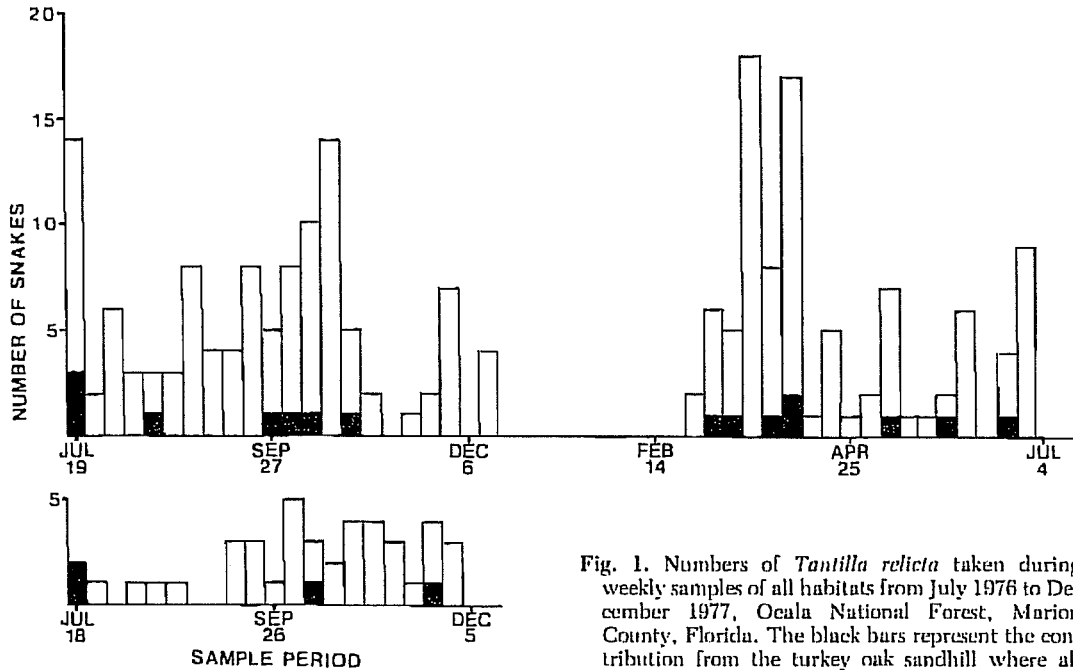


Table 1. *Numbers and percentage frequency of occurrence of 270 prey items in 124 stomachs of Tantilla relicta from Marion County, Florida, 1975-77.*

Prey items	Number of prey items	Percent of prey items	Number of stomachs	Percent frequency of occurrence
Tenebrionidae (larvae)	242	89.6	106	85.5
Chilopoda	17	6.3	16	12.9
Gastropoda	6	2.2	5	4.0
Insecta (legs)	5	1.9	4	3.2

set in from December to February. Trapping for the 5-month period in the second year showed a reduction in the absolute numbers of animals taken, but the activity levels remained essentially the same for corresponding times of year. The *Neoseps reynoldsi* and turkey oak sandhill data seemed to follow these general trends. No temporal differences in activity appeared between the three species.

Food Habits

Identifiable food occurred in 124 (56.6%) of 219 *Tantilla relicta*, 83 (50.6%) of 164 *Eumeces egregius*, and 9 (64.3%) of 14 *Neoseps reynoldsi*. Mount (1963) found 257 (55.9%) of his 460 *E. egregius* with identifiable food. Even though some of the trapped *E. egregius* were probably restricted to a trap for a week or more, they apparently ate selectively of what happened into the traps, and avoided changing their diets or increasing the percentage of empty stomachs. Comparison of stomach contents from *T. relicta* and *N. reynoldsi* with published records and with food data from hand-caught specimens showed that they also did not change their diets significantly on being trapped. No differences in diet composition were observed between different habitats or times of year for a particular

species. Whether an animal was caught in a funnel trap, in a bucket, or by hand made no difference in food items found in their stomachs.

The feeding strategy of *Tantilla relicta* was specialized to the extent that the larva of what is apparently one species of tenebrionid beetle occurred in 85.5% of stomachs with food and made up 89.6% of the numerical total. Centipedes and snails were found only in *T. relicta* and accounted for almost all of the remainder of its diet (Table 1). The diet of *T. relicta* differs from those of *T. gracilis* and *T. coronata*. Force (1935) wrote that *T. gracilis* ate mostly centipedes, along with noctuid, elaterid, and tipulid larvae. Hamilton and Pollack (1956) found that *T. coronata* also fed mostly on centipedes, and occasionally on coleopterous larvae, blattids, and millipedes.

Eumeces egregius fed largely on roaches, spiders, and crickets and on minor amounts of termites, adult and larval beetles, dipterans, sawflies, ants, insect eggs, and earwigs. *Neoseps reynoldsi* stomachs contained primarily beetle larvae, spiders, termites, and antlions.

Food habits comparison between the three species (Table 2) showed two major areas of overlap. Both *T. relicta* and *N. reynoldsi* relied heavily on coleopterous larvae. Conversely, tenebrionid and elaterid larvae were present in

Table 2. *Percentage of total prey items and frequency of occurrence of prey groups in stomachs of Neoseps reynoldsi (n = 9), Eumeces egregius (n = 83), and Tantilla relicta (n = 124), Marion County, Florida, 1975-77.*

Prey group	<i>N. reynoldsi</i>		<i>E. egregius</i>		<i>T. relicta</i>	
	Percent occurrence	Percent total items	Percent occurrence	Percent total items	Percent occurrence	Percent total items
Coleopterous larvae	33.3	13.3	6.0	4.4	85.5	89.6
Rhinotermitidae	22.2	63.3	2.4	2.2	0.0	0.0
Orthoptera	0.0	0.0	63.9	43.8	0.0	0.0
Arachnida	33.3	10.0	43.4	28.5	0.0	0.0

only 6.0% of the *E. egregius*. The other area of overlap was spiders, which were taken in large numbers by both *N. reynoldsi* and *E. egregius*. Roaches and crickets completed the bulk of the diet of *E. egregius*. Termites and antlions occurred in 22.2% of *N. reynoldsi* stomachs with food, but were rarely found in guts of the other two species.

Discussion

None of these three species appear to be a general insectivore, which indicates that natural selection probably has fashioned animals that feed on particular prey in particular microhabitats. The relative abundance of each species probably is not reflected accurately by the Ocala trap data. Pitfalls and funnel traps, by virtue of their construction, tend to trap mostly surficial animals, causing arboreal and burrowing species to be underrepresented. Because of its sand-swimming specialization, *Neoseps reynoldsi* has less chance of being trapped than either *Tantilla relicta* or *Eumeces egregius*. In view of normal field collection data, however, *N. reynoldsi* appears to be considerably less abundant than the other two reptiles. The data support the contention that *E. egregius* is one of the commonest lizards and *T. relicta* is the commonest snake in most of the scrubs and sandhills.

The presence of *Neoseps reynoldsi* in the Ocala turkey oak apparently results from a peculiar set of circumstances. Very small populations probably exist in the scrub, as evidenced by a few specimens collected from this habitat at Central Tower and just north of the junction of Pipeline Road (FR 97) with SR 316 (S. P. Christman, personal communication). After lumbering for longleaf pine, a sandhill may approach the substrate conditions of evergreen oak and young sand pine scrubs, which comprise the preferred habitats for *N. reynoldsi* south of the Ocala Forest. This process seems to have occurred in the Ocala turkey oak; both *N. reynoldsi* and sand pines subsequently colonized from the surrounding scrub. In the past when extensive wildfires (14,200 ha burned in 4 h in 1935) reduced the Ocala sand pine forest to a few patches of mature trees surrounded by large regeneration areas, *N. reynoldsi* was probably as abundant as in its unmanaged habitats south of the Ocala Forest today. Within the Ocala Forest, *N. reynoldsi* is marginally abundant in

the extensive man-induced turkey oak sandhills and very rare in the surrounding scrub.

Food habits reflect microhabitat. Centipedes and snails tend to be superficial in surface litter, whereas termites and antlions are more subterranean. *Tantilla relicta* is found most frequently by raking sand during the day, but this probably reflects its habits at a time when it is not feeding. Considering its chilopodan and gastropod prey, it probably feeds at or above the surface. In view of its food habits and specialized adaptations, *Neoseps reynoldsi* apparently feeds and spends most of its time below the surface. Sand skinks probably take spiders in their own burrows. Telford (1959) collected all but 2 of over 60 *N. reynoldsi* from 5 to 10 cm below the surface. At the turkey oak sandhill trap site, one individual was taken on the surface of an open patch of sand at 1300 h on a sunny day. However, about 20 other specimens were collected by raking them out of the sand. Telford (1959) wrote that his captives fed mostly below the surface.

Eumeces egregius has more generalized food habits than either *Tantilla relicta* or *Neoseps reynoldsi* and seems to take anything small enough to overpower. Moreover, Mount (1963) stated that the Cedar Key Airstrip Island and Seahorse Key populations fed on amphipod crustaceans and dermapterans, respectively. Clearly, *E. egregius* is an opportunistic feeder. Most of its food items are surficial species, and Mount (1963) stated that the data "suggest that most of its food is captured in sheltered situations, perhaps in pre-existing subterranean passages." A reference from Wright and Wright (1957) alluded to all three species. They repeat field notes from O. C. Van Hyning, who had airport workmen at Eustis watch carefully while they were grubbing. Van Hyning wrote, "They took *Tantilla* in the surface layer, *Eumeces egregius* near the surface, but *Neoseps reynoldsi* and *Rhineura* six to ten inches or more down."

Food seems to be the major potential source of competition between these three species, and natural selection apparently has caused such competition to be diminished through microhabitat and dietary differences. *Eumeces egregius* avoids possible food competition by possessing a diet suited to its adaptations as a relatively generalized lizard and by feeding in its near-surface microhabitat. *Tantilla relicta* specializes on a

prey which is unimportant to *E. egregius*, permitting coexistence of both in surficial microhabitats. The food items of *Neoseps reynoldsi* overlap those of both *E. egregius* and *T. relictus*, but competition apparently is reduced by the specialization of *N. reynoldsi* to a completely subterranean existence. *T. relictus* and *E. egregius* are also sand-swimmers. However, this locomotion is probably reserved for different activities than feeding. By swimming in the sand, these three species can escape predation, avoid inhospitable weather, and thermoregulate in exposed sandpiles, such as mounds of the pocket gopher (*Geomys pinetis*) and gopher tortoise (*Gopherus polyphemus*). The dietary differences of these animals indicate that none but *N. reynoldsi* feeds while sand-swimming. The differences in microhabitat and food preferences apparently permit these three species to coexist in the same habitats and to efficiently use the available food resources.

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TECHNIQUES OF COMMUNITY ANALYSIS

Tracking as an Aid in Ecological Studies of Snakes

by

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Abstract

Snakes leave identifiable impressions when crawling over fine-textured soils. Therefore, dirt roads, dunes, and surfaces prepared by abrading topsoil have been used as trackways in ecological studies of snake populations in chaparral and desert in southern California. Preliminary data point to the usefulness of snake tracks in determining relative or behavioral densities, spatial relationships, social behavior, and species composition within communities. In desert sandy habitats, sidewinder rattlesnakes (*Crotalus cerastes*) have been followed for distances exceeding 1.2 km. In a montane chaparral community, it was possible to distinguish tracks made by the three common species, *Crotalus viridis*, *Pituophis melanoleucus*, and *Masticophis lateralis*. Data for snake activity in chaparral point to the difficulties of determining the densities and comparative demographic features of snake populations.

Because of the difficulty of observing and capturing snakes, studies of their ecology have lagged behind that of other vertebrates. It is difficult, often impossible, to enumerate or estimate snake population densities, and community studies may suffer from the lack of equal information for species owing to differences in behavior, population density, and accessibility to the investigator.

Walter Mosauer was probably the first herpetologist to realize that tracks provided convenient records of snakes' activities and that trackways might be used profitably to supplement the scarce opportunities of actual observation. Snakes leave distinct, identifiable impressions when crawling on fine-textured substrate, and these tracks can provide information about the numbers of snakes in an area; time, rate, direction, and extent of movement; social behavior; species composition within a community; and, to some degree, individual recognition. Yet, apart from early descriptive studies, a tracking approach has not been widely applied in quantitative ecological studies by herpetologists

(see Mosauer 1933; Cowles 1949; Bider 1968). In studies of other animals, most notably mammals, tracking methods have been adopted to determine home ranges and activity patterns, as well as to census populations. Population estimates based on tracking can be highly precise and are considered superior to estimates based on trapping alone (e.g., Marten 1972).

The intent of this paper is to stimulate interest in the development and application of tracking methodologies in ecological studies involving snakes. The discussion is aimed at identifying some potential applications of tracking methods in the light of two case studies in desert dune and montane chaparral ecosystems. I also comment on some of the difficulties of determining densities and demographic units within snake populations.

Sidewinder Studies at Kelso Dunes

The fine-grained sands of desert dunes provide unique opportunities for studying the daily movements of snakes, especially those of "sidewinder" vipers which occur (sometimes abundantly) in dune habitats of low latitude deserts.

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The following account is based on unpublished data from Brown (1970), who studied a population of *Crotalus cerastes* at Kelso Dunes in the Mojave Desert of southern California from June 1967 to June 1969.

The study area was a 7-ha grid of windblown sand at the easternmost edge of the Devil's Playground sand sea, roughly 4 km SSE of Kelso, San Bernardino County, California. The fine sand at this locality is 2 to 3 m deep but becomes progressively shallower to the east, where the dunes finally give way to the sloping alluvial fan of the Providence Mountains. A matrix of rather uniformly spaced creosote bushes (*Larrea divaricata*) form nuclei for prominent accretion dunes on the study grid proper; other vegetation comprises a denser assemblage of low-growing plants such as galleta grass (*Hilaria rigida*), burroweed (*Franeria dumosa*), and sandpaper-leaf (*Petalonyx thurberi*).

Sidewinder tracks are made as a progressive series of parallel impressions, each one terminating in the hook of a "J" (see Gans 1970). The hook is formed by the head of the snake and indicates the direction of travel. In ideal circumstances, the length of a track should exactly equal that of the sidewinder (Klauber 1956). However, a number of comparisons using snakes caught in the field showed that this was not always the case; most tracks varied from 3 to 5% shorter than the snakes which had made them. However, because this error is quite small, the tracks of this species can be used to determine the directions of movements of individuals and the size composition of a population.

Tracks at the Kelso study site were readily located by walking the length of the study grid in a series of parallel traverses in the early morning. Tracks may become obliterated or erased during the day due to wind and the unfavorable angle of sunlight. If any part of a trackway entered the grid, it was mapped for its entire length, thus providing detailed information on sidewinder movements. Trackways found outside the grid were also mapped for comparative data on length and direction. Frequently, the sidewinder that had made a given trackway was found and could be observed or captured. Metal rods were used to mark the start and finish points of trackways, and this allowed monitoring the progressive movements of individual sidewinders over periods of several days. For each trackway, both the total length and the

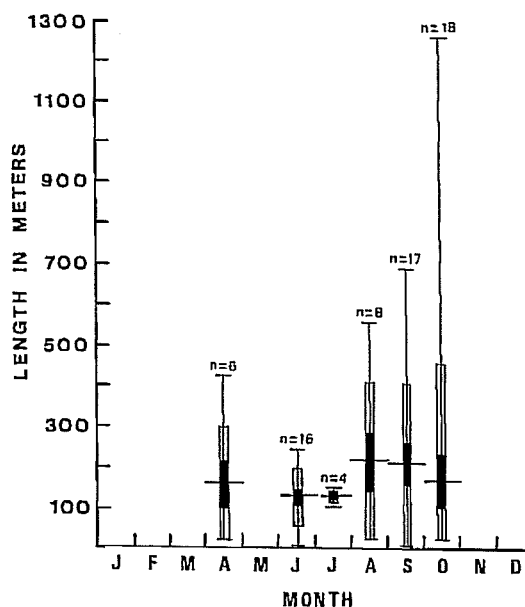


Fig. 1. Lengths of sidewinder trackways measured during 1967-69 on the Kelso study site, plotted by month. Vertical bars denote one standard error (black) and one standard deviation (white) on either side of the mean (horizontal line). (After Brown [1970], with permission.)

straight-line distance from start to finish were recorded.

Tracks were found on the study site from April to October and provided a quantitative record of sidewinder activity during the two years of study. Trackways in June and July averaged somewhat shorter than those of earlier spring or fall; the longest trackways were recorded during the cooler months (Fig. 1). However, trackways of a given individual were not necessarily uniform in length or of increasing distance on successive nights. Nor was direction consistent, either for the population or for individuals. Occasionally, individual sidewinders moved long distances in short periods. For example, the longest trackway made by a sidewinder in a single night of wandering was that of an adult snake which on 13-14 October moved a total distance of 1,260.2 m. Few juvenile trackways were mapped, but they were said to be shorter than those of adults. The total length of a trackway usually was less than twice the straight-line distance between start and finish points.

Brown suggested that sidewinders probably wandered randomly without home ranges or with home ranges considerably larger than those of the few crotalids that have been studied intensively (e.g., Fitch and Glading 1947; Fitch and Shirer 1971). My own impressions during visits to Kelso Dunes were that sidewinders there typically followed the "path of least resistance" (e.g., between shrubs, in low places between accretion dunes, etc.) without purposeful exploration, as in cases where tracks progress from shrub to shrub or from burrow system to burrow system.

Some of the early observations of sidewinders were made by Mosauer (1933) who trailed these snakes over the sand dunes of the Coachella Valley, California. He found that the tracks made in a given night often would trend in a particular direction for as much as 305 m, and the snake was often found coiled at the base of a plant at the end of the track. Mosauer surmised that after a few nights of wandering the snakes possibly might return to their starting point. Brown's data fully support Mosauer's on the wandering inclinations of sidewinders and the distances they travel. However, only once was a sidewinder observed to return to its starting point after a night of wandering, and it seems doubtful that this occurs very often in this species. On the other hand, the western diamondback rattlesnake (*Crotalus atrox*), formerly found in the Coachella Valley along with the sidewinder, apparently does have a homesite to which it returns each morning (Mosauer 1935).

Studies on the 7-ha grid showed that from two to five trackways were found there daily from April to October. This indicates a variable surface density of from 0.29 to 0.71 active sidewinders per hectare. These figures are almost certainly underestimates of the actual population density on the Kelso Dunes, for a significant percentage of the population might not be active on the surface during a given measurement period. In Brown's study, the grid was worked by a single person, and it was difficult to follow individuals for long periods. Given sufficient manpower, however, it should be possible to follow the sequential movements of individual snakes over a significant period of the active season and enumerate directly the active population. Very likely the population on the 7-ha grid is largely transient and may fluctuate in density over

rather short periods of time. This dynamic aspect of the population structure would be difficult to assess from conventional mark and recapture techniques.

A very important implication of the trackway studies at Kelso Dunes is that, given a randomly mobile population wherein some individuals elect to disperse relatively long distances, even marginal estimates of density based on mark and recapture methods may be impossible to obtain. In the sidewinder study at Kelso, 53 sidewinders were marked over the 2-year period. Of these, only six were recaptured and only two were recaptured more than 5 days after being released.

Tracking Snakes in Chaparral

Tracking offers a promising approach for ecological studies in a variety of habitats where vegetation density and climate are not major constraints. Tracking is possible on a variety of fine-textured soils, and even coarse or hardened surfaces can be modified for tracking purposes. In areas of moderately dense vegetation, tracks can be sampled from strips or patches of cleared substrate. For example, snakes have been studied in Quebec using fine sand transects constructed in woods and fields, protected from rain by a canopy (Bider 1968).

Since 1971, effort has been directed toward comparing the abundance of active snakes in burned and unburned patches of chaparral in San Diego County, California. This study is still in progress, and the purpose here is not to report conclusions but to suggest directions; throughout the study I have attempted to identify situations in which tracking might offer practical advantages as a field method in herpetological investigations.

Sampling Techniques

The use of tracks to quantify the activity and relative abundance of snakes was stimulated initially by the hypothesis (corroborated by cursory field observations) that snake populations were reduced in burned habitat either as a direct or indirect consequence of fire. Snakes are not easily observed, and, especially under conditions of low population density (or activity), the "catchability" of specimens diminishes significantly. However, sampling is



Fig. 2. A road bearing excellent tracking surface in remote chaparral (San Diego County, California).

always possible by tracking; if any number of snakes are active, their tracks will be evident.

I have used dirt roads as transects for sampling tracks in chaparral habitats. Distances exceeding 2 km in each of burned, unburned, or ecotone chaparral were censused two or three times daily for variable periods during seasons of peak snake activity (May–July). Each transect was traversed in both directions during a given census to allow optimal visibility of tracks, which depends on the direction of oblique lighting, particularly when the sun is low. Tests demonstrated that even the smaller snakes of the area (e.g., juvenile *Hypsiglena torquata*) left detailed impressions when crawling upon the surfaces of dirt roads that were used in the study. Information about the size, species, and direction of a snake's travel was easily obtained from inspecting tracks that were found on the transects. Counts of tracks can potentially be used to quantify the relative abundance and species densities of active snakes and can provide de-

tailed information about the spatial and temporal aspects of activity. Moreover, different areas can be sampled simultaneously, thus enabling one to investigate the geographic synchrony of activity patterns.

Dirt roads traverse remote areas of chaparral in California and permit extensive sampling of habitat (Fig. 2). Many of these roads are adequate for tracking except in areas having very coarse soils or where motor vehicle traffic is excessive. Some motor vehicle traffic is actually desirable because it creates and maintains a fine-textured substrate. Even where the investigator elects not to use tracking as a principal method of study, much preliminary information regarding abundance, species composition, etc. might be obtained in a short period from track counts on roads.

In a study of snake movements in eastern Kansas (Fitch and Shirer 1971), it was shown that snakes sometimes avoided crossing roads. This appears not to be a problem in chaparral

where the vegetation forms a much less continuous ground cover (at substrate level) than in the more mesic habitats of eastern Kansas. In chaparral, the number of tracks on dirt roads compared favorably with the number of tracks occurring on narrow (1 m) strips of tracking substrate in off-road habitats where natural breaks in vegetation equalled or exceeded the width of the tracking substrate. Moreover, out of hundreds of observations of tracks in chaparral, the number of occasions where a track indicated that a snake approached or entered upon a road and then reversed its direction was extremely rare ($< 1\%$ of observations). I have observed several situations in which snakes crossed dirt roads repeatedly during day-to-day wanderings within a specific home range.

In addition to roads, tracking surfaces can be prepared *in situ* wherever there is sufficient exposed soil. Brushing or scraping the ground with a heavy pushbroom creates suitable substrate by removing large debris and abrading coarse surfaces. These "scrubbing" procedures have been used to create strips and grids of trackway in several areas of chaparral (Fig. 3). The "grids" of trackway were not arrayed in a regular geometry. Tracking surfaces comprising a grid followed the natural openings between shrubs and rock (usually a few meters apart) and were spaced so that movements of any snake within a unit area of habitat could be detected.

In this manner I have monitored the occurrence of tracks on 0.5-ha grids for relatively short periods (one to several weeks). Although it was not possible to enumerate snake densities on these sites owing to the limited time and area sampled, the observations did demonstrate the feasibility of relating tracks to habitat area, even in relatively dense brush. I was able to follow the movements of individual snakes on these grids, and I was able to identify and even capture them. More intensive efforts at tracking a larger area would enable an investigator to quantify the numbers (but see below), kinds, and activity of snakes in a given patch of habitat.

Identifying Snakes from Their Tracks

In chaparral, snake tracks have distinct characteristics, and the trained observer can distinguish these from other marks or impressions that tend to resemble those of



Fig. 3. Tracking strips (arrows) created by scraping and brushing topsoil in (A) recently burned chaparral and (B) chaparral 15 years or older.

snakes. If a dirt tracking surface has a sufficiently fine texture, a fresh snake track (age < 18 h) appears reflective or lustrous, especially when viewed obliquely. This quality is attributable to the compression of substrate particles by the snake's weight during efforts at locomotion. Lizard tracks usually can be distin-

guished by the presence of foot impressions and the low reflectance quality (lack of sheen or luster) of the tail drag (Fig. 4A). However, the foot impressions may be obscured or even absent in certain circumstances. Tracks of the lizard *Gerrhonotus* spp. (and probably large scincids in other habitats) are an exception to this generalization, as the body and the tail produce a lustrous track. In these cases, however, impressions of feet and even digits are usually well preserved. Ant trails may superficially resemble snake tracks, but the dirt lacks compression and the high reflectance (luster).

It is widely known that tracks of vipers which sidewind on desert dunes are easily recognized owing to their unique mode of locomotion. It is also possible to identify tracks which are produced by snakes having less unique and even similar locomotory modes. In the chaparral near Mount Laguna, San Diego County, California, I have been able to identify tracks made by rattlesnakes (*Crotalus viridis*), gopher snakes (*Pituophis melanoleucus*), and striped racers (*Masticophis lateralis*). An account follows of the criteria by which the tracks of these three species might be distinguished.

Pituophis melanoleucus (Fig. 4B). This snake typically progresses in a rectilinear or concertina mode (for terminology, see Gans 1970). Consequently, the tracks of this snake are quite straight but sometimes exhibit abrupt curvatures where force transmission is directed backward. The body presses firmly against the substrate, and the tracks of this snake are normally continuous throughout their length.

Crotalus viridis (Fig. 4C and D). The tracks of this snake are readily distinguished from those of sympatric non-crotalid species. Identifying features are attributable to the weight of these snakes and their habit of carrying the rattle erect. The track may be straight or sinuous but is almost always unbroken, and the soil is pressed firmly. The track is often deep and typically appears as though several snakes had traversed the same region of substrate. This effect seems to be caused by the sliding of the body as the snake attempts to gain traction during efforts at undulating. The trailing end of the snake is broad and blunt owing to the erect position of the rattle, and the tail at the base of the rattle forms a broad depression within the width of the main track. "Tail drags" are also seen in tracks of other snakes, but only in rattlesnakes are they

relatively broad in relation to the width of the entire track.

Masticophis lateralis (Fig. 4E and F). The track of this species is distinguished from the previous two because it undulates broadly and is usually discontinuous. Ridges and depressions formed at points of force transmission are deep and sharply defined, and tail drags often cross the main track obliquely.

Snakes can sometimes be found by searching in the immediate vicinity of freshly-made tracks, particularly if searches are conducted along dirt roads during peak hours of snake activity. I have used this collecting procedure to affirm empirically my ability to identify tracks of rattlesnakes, gopher snakes, and striped racers. Snakes were identified correctly in 100% of 30 accumulated cases where track identifications were subsequently verified by capturing the snake. Clearly, more data are needed to establish the reliability of track identification, but the method at least appears promising. The three species of snake mentioned here include the more common or conspicuous snakes in the Mount Laguna chaparral and account for 90% of all snakes that were seen or collected during a 3-year period. It may be possible to identify the tracks of at least some of the other snakes present in chaparral, but I have had limited opportunity to observe them.

In cases where identifications are uncertain, tracks might be assigned to species on the basis of probability values. For example, two species of rattlesnake can be found in the Mount Laguna area: *C. viridis* and *C. mitchelli*. The latter species is relatively uncommon in certain areas, and in the locality where my studies were conducted, it accounted for only 2 out of 48 rattlesnake sightings during a 3-year period. In this example, it seems reasonably secure to assume that something in excess of 90% of *Crotalus* tracks result from the activity of *C. viridis* (assuming that tracks of *C. viridis* and *C. mitchelli* are indistinguishable). Intensive sampling would presumably allow one to develop a more rigorous quantitative basis for assigning to species tracks that are potentially ambiguous. Further research on the species specificity of track characters seems potentially valuable at this time.

An alternative procedure is to assign "ambiguous" tracks to ecological guilds of snakes rather than to species. Rattlesnakes and racers are

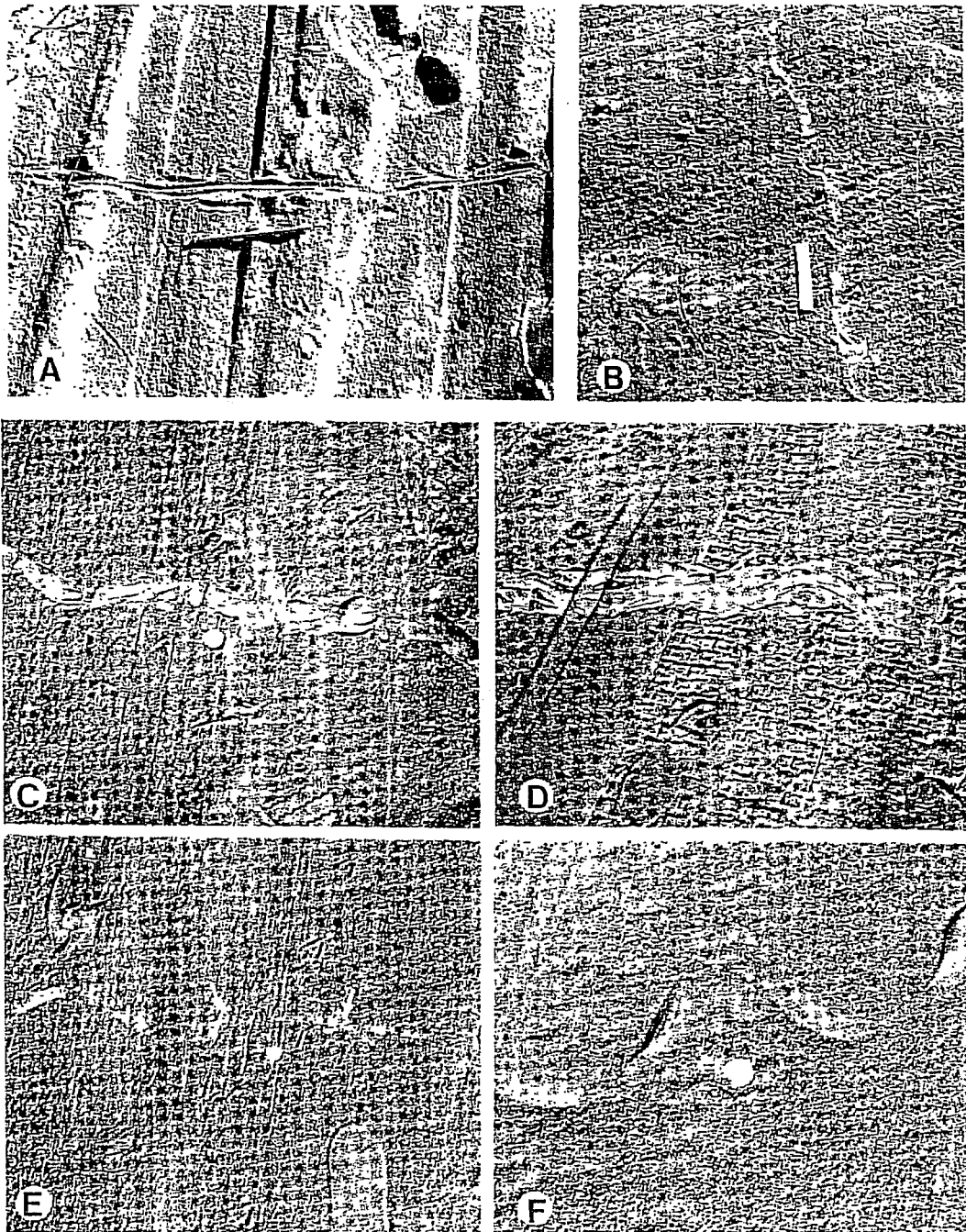


Fig. 4. (A) Lizard tracks (probably *Cnemidophorus tigris* and *Uta stansburiana*) illustrating feet impressions and low-reflectance quality due to the "drag" of the tail. (B) Track of adult *Pituophis melanoleucus* illustrating the effects of concertina as well as rectilinear locomotion. (C and D) Tracks of adult *Crotalus viridis* (note tail impressions within the main track). (E and F) Tracks of adult *Masticophis lateralis*. Note the discontinuity of the track, sharp ridges, and oblique tail drags (arrows).

examples of two possible categories. This level of resolution might be adequate for certain kinds of ecological investigations.

Although in small mammal tracking it is possible to recognize individuals which have been toe-clipped or banded, the possibility of recognizing large numbers of tagged snakes from individual tracks is unlikely. However, it is possible to recognize the tracks of a small number of individually tagged snakes from drag marks produced by metal bands which are attached to a posterior scute (unpublished observations); such identifications could be useful in limited circumstances. Snakes may frequent a specific area, at least during certain periods, and will often move in regular circuits within a "home range" of habitat. Thus, a localized, repeated spatial pattern of identically shaped tracks probably denotes a particular individual. I have confirmed this by repeatedly capturing scale-clipped snakes which were identified and subsequently relocated by tracking. Such snakes conceivably could be tagged once for individual track recognition and then followed without further disturbance. Individual tagging could also be useful in distinguishing the tracks of a limited number of resident animals from those left by "transients" on a particular plot. Several snakes could possibly be recognized individually by varying the width or number of bands attached to scutes.

Social Behavior

Documented aspects of the social behavior of snakes usually are related to reproduction, aggression, or denning activities. There is limited information on whether snakes move in social groups during the active season, but such behavior conceivably could be learned from tracks. Numerous and systematic observations of tracks in chaparral indicate that snakes occasionally move in pairs. When crossing roads, snakes usually leave a track which is more or less perpendicular to the length of the road and which is not associated with other impressions. Occasionally, two (and rarely three) tracks occur together and have topographies indicating that one snake had crawled almost directly over the track of another. I interpret these tracks to indicate purposeful social behavior, possibly related to sexual pairing and mediated by chemical (pheromone) communication. On one occasion, search for the snakes associated with

such a "double track" revealed two adult *C. viridis*, a male and a female, lying together in a loose coil beneath a shrub. These snakes were perfectly immobile and not engaged in any overt sexual activity. The snakes were observed for about 15 min and then disturbed for the purpose of making positive sex identifications (by probing the tail with a blunt instrument). In another instance, two adult *M. lateralis* were observed only a few meters apart when I followed a "double track" offroad into an area of grass and oak trees. Only one of the snakes was captured.

Double tracks were found during spring and summer, suggesting that pair associations might not be limited to periods of courtship and copulation. Other observations indicate that the same individual snake will crawl repeatedly over the exact same route. In view of these findings, studies of pheromone trailing behavior in snakes, now well documented in the laboratory (Gehlbach et al. 1971; Ford 1975; Kubie and Halpern 1975), might profitably be extended to natural situations.

One other observation is noteworthy. In the late morning of 26 July 1973, eight tracks appeared on a short distance of road (approx. 5 m) within a brief period (believed to be less than 1 h and probably no longer than a few minutes). All of these tracks were identical in size and topography, and they all indicated a common direction of movement away from a grassy meadow toward a tree-covered hillside. Searching the nearby hillside eventually produced one adult *Coluber constrictor*, but no other snakes were found. Two of the eight tracks were made during the few minutes while searching efforts were in progress, and four of the other tracks occurred in pairs (two sets of double tracks). The identical appearance of these tracks suggested that all of the snakes were about the same size and probably belonged to the same species, while their temporal and spatial occurrence suggested that there was group structure to the movements of these eight individuals.

The recent discussion of social behavior in juvenile green iguanas by Burghardt et al. (1977) focuses attention on complex social patterns in reptilian groups. Interest in this subject might profitably be extended to snakes, as indicated by accounts of denning activities (e.g., Woodbury et al. 1951; Klauber 1956), communal egg-laying (Brodie et al. 1969; Gregory 1974;

Palmer and Braswell 1976), and unexplained non-wintering aggregations (e.g., Kropach 1971). From the tracking observations, it may be inferred that a significant amount of snake movements has social structure. With rigorous tracking efforts, it should be possible to follow through time the social interactions between known individual snakes residing on tracking grids in natural environments.

The Dynamics of Snake Populations

Almost all present knowledge concerning the population ecology of snakes has been generated by capture—recapture analysis. Turner (1977) recently evaluated density estimates for snakes and concluded that the reliability of these measures is questionable in almost all cases. What seems to receive little attention is the blunt fact that even the best estimates relate only numbers of surface-active snakes to a specific area at a particular time. We do not know how accurately these estimates reflect absolute density, considering the environment in three dimensions, or whether the numbers of individual snakes registered comprise a natural demographic unit. In areas of low population size (or activity), density estimates based on capture—recapture methods have unacceptably large variances, and problems related to the “catchability” of snakes frequently invalidate the assumptions which underlie the analysis.

There are no easy solutions to these problems. However, in appropriate habitats tracking might improve our capacity to capture individual snakes and reveal more directly the temporal variability of activity. Tracks might also assist in determining whether snakes belonging to a particular species or locality are widely dispersing (e.g., *C. cerastes*) or are structured demographically into more localized units. Tracking techniques would be of tremendous value in attempts to enumerate densities of snakes by their removal.

Some of the sampling problems in relation to density estimates are suggested by reference to Fig. 5, which depicts counts of snake tracks determined in two successive years at the same locality near Mount Laguna. The number of tracks that were evident in 1973 greatly exceeded those of the previous year (e.g., there was nearly an eight-fold increment of tracks which were 1.0 to 1.5 cm in width). Size classes

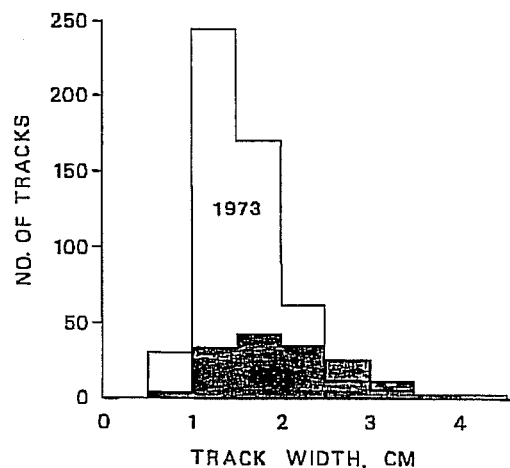


Fig. 5. Counts of snake tracks from 2 km of dirt road during 16 days within the period 15 June to 15 July in two successive years.

of tracks were arbitrarily delimited and reflect measurements of average width. Generally, hatchling or yearling snakes produce tracks smaller than 1 cm wide. The data in Fig. 5 indicate that the increment of snake activity observed in 1973 cannot be attributed to a recruitment of young born the previous year. Changes in the number of tracks must reflect either changes in the number of active snakes or changes in the activity of individual snakes, or both. Observations of the characteristics of tracks in relation to their temporal and spatial occurrences indicated that the differences in numbers of tracks reflected, at least in part, changes in the number of active snakes.

How can we account for the differences in snake behavior observed during these two years? In 1972 precipitation was far below normal, and conditions were much drier than in 1973 (winter precipitation in 1972–73 exceeded that in 1971–72 by more than fourfold, Keeley 1977). Whether habitat aridity produced the observed changes in snake activity between 1972 and 1973 cannot be concluded unequivocally, but the correlation is compelling. The relationship between increased precipitation and increased snake abundance has been noted elsewhere (e.g., Conant 1938; Fitch 1965; Clark 1970). It can be hypothesized that dry conditions suppress activity in “dry” years or that excessively moist conditions stimulate activity in “wet” years, or both.

An important implication of these data is that

changing climatic conditions may cause snakes to spend much (perhaps all) of the active season in seclusion where they are inaccessible to capture or observation. If this is so, changes in the densities of snake populations reported over time (e.g., Klimstra 1958; Fitch 1965; Clark 1970; Prestt 1971; Parker and Brown 1973) may merely reflect changes in activity (behavioral density). It is inaccurate to refer to such phenomena in terms of absolute densities unless the spatial or activity limitations are specified. Clearly, many species of snakes might conduct feeding and other essential activities within spatial dimensions of habitat inaccessible to the human observer, and this could also account partially or wholly for the reported "rarity" of certain species. Energy budgets of ectothermic vertebrates permit prolonged periods of dormancy; periods in which aboveground activity is negligible or absent are known to exceed a full year in amphibians (Mayhew 1965) and in lizards (Turner et al. 1969). The above discussion emphasizes the difficulty of studying the comparative demography of snakes.

Another interesting feature of the data in Fig. 5 is the small proportion of tracks that includes yearling snakes (tracks 0.5 to 1.0 cm wide). The inferred low activity of snakes in this size class, at least in certain seasons, possibly accounts for the more general observation that younger-aged snakes are under-represented in collections from live traps (Fitch 1963a, 1963b; personal communication; Hirth and King 1968). For this reason alone, many estimates of the age structure as well as density of snake populations are likely to be inaccurate. The diminished activity of younger snakes, relative to adults, may be related to avoidance of exposure to higher rates of predation, avoidance of higher rates of evaporative water loss due to less favorable surface-mass ratios, and possibly frequent feeding to maximize growth (snakes digesting food tend to be inactive). Dispersal in snake communities thus may be accomplished by older rather than (or in addition to) younger individuals, as is suggested in Brown's study (1970) of sidewinders.

In summary, I share completely Turner's (1977) skepticism about our present capacity to estimate population densities of snakes. While it appears feasible to relate numbers of active snakes to both time and spatial dimensions of habitat, there is great difficulty in determining qualitatively and quantitatively the proportion

and elements of the total population structure which have actually been sampled. Hopefully, these deficiencies can be improved with the application of intensive and more sophisticated effort in ecological research. Particular attention should be paid to the subterranean ecology of snakes. In aboveground studies, tracking can improve sampling and provide detailed resolution of activity patterns in terrestrial communities.

Acknowledgments

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Field Techniques for Herpetofaunal Community Analysis

by

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Abstract

A standardized amphibian and reptile trapping system is described and compared with other survey techniques. The new sampling system has proven very effective for sampling small, secretive, terrestrial species, but must be used in conjunction with other more conventional techniques to obtain a complete herpetofaunal species list.

Over the past several years we have had the opportunity to undertake several intensive herpetological sampling programs and to employ and evaluate a variety of sampling techniques in different habitat types in Florida. In the course of these studies we have developed and standardized a trapping system that we believe can be employed in many terrestrial habitats. The data obtained from this technique allow estimates of species richness and provide an index of the relative abundance of most common terrestrial amphibian and reptile species. The technique by itself, however, does not reliably sample all species in a habitat and must therefore be coupled with specific search techniques for those species less likely to be taken in the trapping system. The combination of our trapping method and the appropriate specific search technique will, however, provide a maximum amount of information on the amphibians and reptiles in any specific region with a minimum amount of effort. Here we describe our array system and compare it with other herpetofaunal sampling techniques. A similar system has been developed independently by Vogt and Hine (this volume).

Array System

Our sampling array is a system of pitfall and

double-ended funnel traps placed in conjunction with drift fences which divert moving animals into the traps (Fig. 1). The drift fences are 7.6-m lengths of 46-cm-high "valley tin" arranged in a plus-shaped pattern with a central separation of 15 m. Each arm has a 19-L plastic paint bucket sunk flush with the ground at each end. The tin fence overhangs the bucket slightly and fits into a slot cut into the plastic bucket. A masonite board raised 2 to 4 cm above the lip of the bucket provides shade and keeps rain and litter out. In most soil types (including loose sand) support stakes are not needed; simply burying the fence about 10 cm into the ground keeps it firmly upright.

The funnel traps are constructed of 76-cm aluminum window screening rolled into a cylinder about 20 cm in diameter. Funnels are fashioned out of 38- x 38-cm screening and inserted into each end of the cylinder. The whole trap is assembled with ordinary office staples. Specimens can be removed with forceps or tongs through either end. The funnel traps are placed flush with the ground and appressed to the tin fence, one on each side of each arm. Loose soil or ground litter is brushed into the mouth of the traps to create a more natural entry. A masonite board is placed against the fence over the trap to provide shade.

A team of three field persons can, with a little practice, install a complete array in 1-2 h, depending on the habitat. The four drift fence arms are staked out at right angles to each other

¹Deceased: Died at Gainesville, Florida, on 10 December 1981.

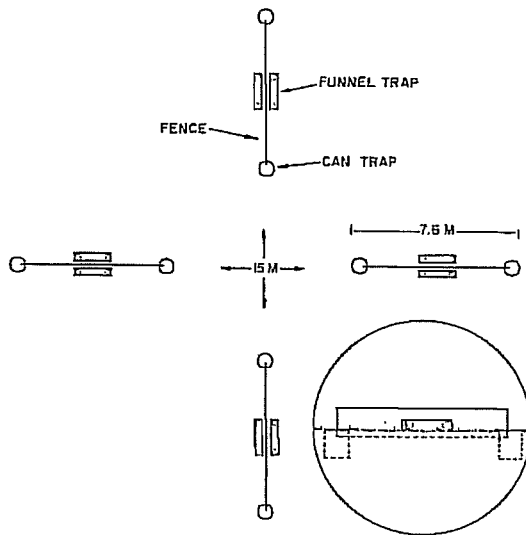


Fig. 1. Standard amphibian and reptile sampling array system.

and a trench is dug for each arm. The bucket holes are then dug on each end of the trench and the buckets installed. As two people hold the fence up in the trench, a third person fills the soil back in, packing it down as he proceeds, using alternate downward pressure from the right and left foot.

After 22 months, 20 arrays in the Ocala National Forest, Florida, are still operating and have required virtually no maintenance. The buckets and fences do not rust and the pressure-treated masonite is not damaged by insects. The total cost of materials is about \$65 for each array.

Because the arms of an array are at right angles to each other, no directional bias is introduced by its placement. Thus arrays can be constructed at random locations without regard to natural animal migration routes and yet still intercept moving animals coming from any direction. Our standard procedure is to install two arrays a minimum of 100 m apart in a habitat type. The traps are checked once a week, and although the shrews and mice are usually dead, the arthropods, amphibians, and reptiles are generally in good condition and can be marked and released or saved as desired.

During the Cross Florida Barge Canal Wildlife Restudy (Florida Game and Fresh Water Fish Commission 1976), we operated 30 arrays for a total of 7,432 array-days in 11 different habitat types. These traps collected 1,644 speci-

mens of 43 species of amphibians and reptiles for an average of 0.22 specimen per array-day, or 1.55 specimens per array each time they were checked (Table 1). The relative effectiveness of the funnels versus the buckets in an example site can be seen in Fig. 2.

These data are of considerable importance in comparing faunal associations in a study area. The can-trapping technique has inherent biases for certain types of animals. Species that are agile climbers (e.g., treefrogs [Hylidae]) may escape from the traps and are seldom taken. Similarly, large snakes may enter and leave the can traps at will; however, large snakes and occasionally treefrogs are taken in the funnel traps. Masonite can covers generally exclude turtles with the exception of an occasional small specimen. Overall, the arrays tend to select for the smaller surface-active amphibians and reptiles as well as terrestrial arthropods and shrews and rodents. One species, the introduced greenhouse frog (*Eleutherodactylus planirostris*), appeared to have a positive orientation to the cans as refuges and congregated in them in large numbers even though capable of climbing out at will. Can traps are unsuitable for use in habitats where the soil is fully saturated or for use below the ground water level. However, in these sites we replace the buckets with larger diameter funnel traps made of window screening, which our preliminary results suggest are almost as effective as the buckets.

The data collected by the array system can be used in a variety of ways to characterize and compare habitats. Besides generating species lists, arrays provide a clear indication of relative abundances between habitat types (Fig. 3). Species diversity indices can be calculated for the samples, and species richness and abundances can be compared across habitat types (Table 1). Seasonal patterns in surface activity may become readily apparent (Fig. 4). The specimens collected can be used to estimate reproductive patterns, growth rates, age-class representation, biomass relations, food habits, and infraspecific variability.

Other Can-trapping Methods

During the study, we also tested several other types of pitfall trapping systems. All were set within 500 m of the standard arrays in the same

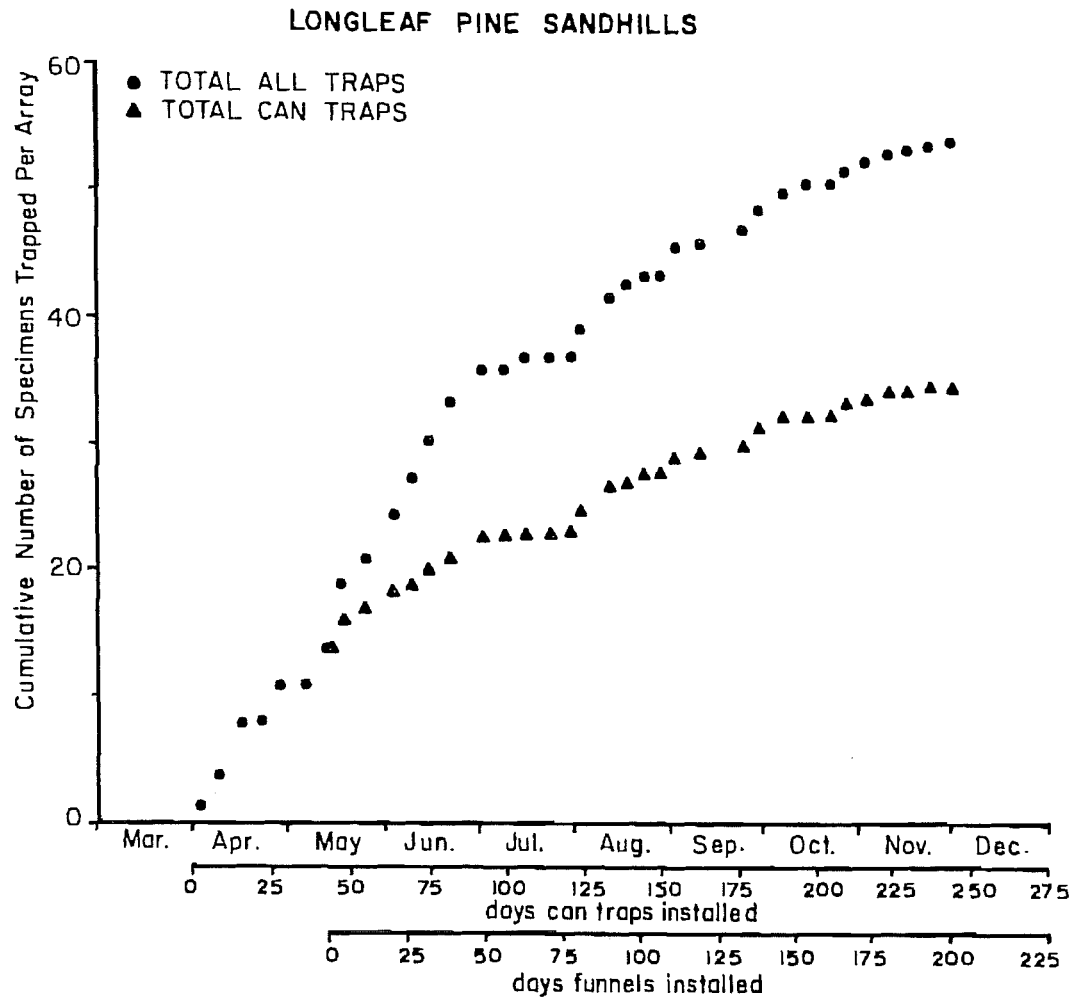


Fig. 2. Relative effectiveness of funnel traps versus can traps in longleaf pine sandhills, Florida.

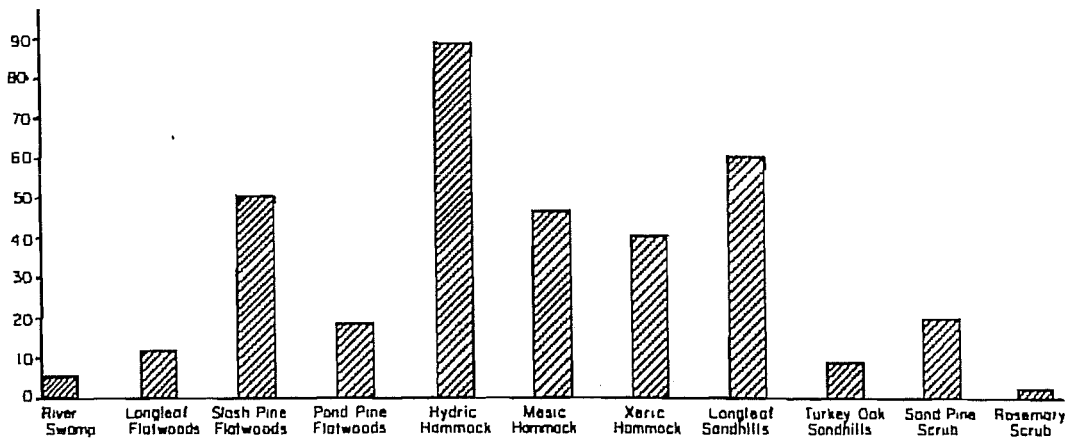


Fig. 3. Total number of *Gastrophysa carolinensis* ($\times 1,000$) trapped per array-day by the standard array system during the Cross Florida Barge Canal Wildlife Restudy in 11 different habitat types.

Table 1. Total numbers and adjusted relative values (individuals per array per day \times 1,000) of amphibians and reptiles trapped in 30 arrays in 11 sites along the route of the proposed Cross Florida Barge Canal (Florida Game and Fresh Water Fish Commission 1976).

Species	River swamp				Pond		Turkey				Total	
	Longleaf flatwoods	Slush flatwoods	pine flatwoods	Hydric hammock	Mesic hammock	Xeric hammock	Longleaf sandhills	oak sandhills	Sand pine scrub	Rosemary scrub	all sites	
<i>Eleutherodactylus planirostris</i>	—	151(163.4)	89(305.8)	—	—	438(944.0)	—	1(0.9)	—	—	679(91.2)	
<i>Kinasternon bauri</i>	—	—	—	1(1.9)	—	—	—	—	1(0.9)	—	2(0.3)	
<i>Rhineura floridana</i>	—	—	—	—	—	—	—	—	1(0.9)	1(1.8)	2(0.3)	
<i>Anolis carolinensis</i>	—	1(1.1)	—	7(13.4)	9(19.4)	10(25.6)	4(5.4)	5(4.6)	6(5.6)	3(5.5)	45(6.0)	
<i>Sceloporus undulatus</i>	—	3(3.2)	—	—	—	—	—	9(8.2)	—	1(1.8)	13(1.8)	
<i>S. woodi</i>	—	—	—	—	—	—	—	—	1(0.9)	—	1(0.1)	
<i>Cnemidophorus sexlineatus</i>	—	—	—	—	—	—	9(12.2)	3(2.7)	3(2.8)	19(34.8)	34(4.6)	
<i>Ophisaurus ventralis</i>	—	—	—	—	—	—	—	1(0.9)	—	—	1(0.1)	
<i>Eumeces egregius</i>	—	—	—	—	—	—	—	14(12.8)	3(2.8)	14(25.6)	31(4.2)	
<i>E. inexpectatus</i>	—	14(15.2)	—	—	—	2(5.1)	19(25.7)	16(14.6)	28(26.0)	10(18.3)	90(12.1)	
<i>E. laticeps</i>	—	—	1(3.4)	1(1.9)	—	4(10.3)	—	—	—	—	6(0.8)	
<i>Scincella laterale</i>	—	27(29.2)	2(6.9)	20(38.2)	16(34.5)	3(7.7)	38(51.5)	31(28.3)	18(16.7)	1(1.8)	159(21.4)	
<i>Cnemidophora coccinea</i>	—	—	—	—	—	—	—	—	4(3.7)	3(5.5)	7(0.9)	
<i>Coleuber constrictor</i>	—	—	—	—	—	—	—	—	1(0.9)	2(3.7)	3(0.4)	
<i>Diadophis punctatus</i>	—	—	1(3.4)	3(5.7)	—	—	—	—	1(0.9)	—	5(0.7)	
<i>Heterodon simus</i>	—	—	—	—	—	—	—	2(1.8)	—	—	2(0.3)	
<i>Masticophis flagellum</i>	—	—	—	3(5.7)	—	—	—	1(0.9)	—	1(1.8)	5(0.7)	
<i>Pituophis melanoleucus</i>	—	—	—	—	—	—	1(1.4)	—	—	—	1(0.1)	
<i>Storeria occipitomaculata</i>	—	—	—	1(1.9)	—	1(2.6)	—	—	—	1(1.8)	3(0.4)	
<i>Notophthalmus perstriatus</i>	—	—	—	—	1(2.2)	—	—	—	—	—	2(0.3)	
<i>Plethodon glutinosus</i>	—	1(1.1)	—	3(5.7)	—	—	—	—	—	—	3(0.4)	
<i>Scaphiopus holbrooki</i>	—	17(18.4)	—	18(34.4)	17(36.6)	8(20.5)	5(6.8)	1(0.9)	3(2.8)	2(3.7)	73(9.8)	
<i>Gastrophryne carolinensis</i>	1(6.9)	12(13.0)	15(51.5)	47(89.7)	22(47.4)	16(41.0)	45(61.0)	10(9.1)	22(20.4)	2(3.7)	195(26.2)	
<i>Bufo quercicus</i>	—	2(2.2)	—	—	—	—	—	—	1(0.9)	1(1.8)	21(2.8)	
<i>B. terrestris</i>	3(20.8)	28(30.3)	1(3.4)	5(9.5)	13(28.0)	8(20.5)	6(8.1)	6(5.5)	32(29.7)	10(18.3)	115(15.5)	
<i>Acris gryllus</i>	—	—	—	—	—	—	1(1.4)	—	—	—	1(0.1)	
<i>Hyla cinerea</i>	—	—	—	—	1(2.2)	—	—	—	—	—	1(0.1)	
<i>H. crucifer</i>	—	—	—	1(1.9)	—	—	—	—	—	—	1(0.1)	
<i>H. femoralis</i>	—	2(2.2)	—	—	1(2.2)	—	—	—	—	—	3(0.4)	
<i>H. gratiosa</i>	—	—	—	—	—	—	—	—	1(0.9)	—	1(0.1)	
<i>H. squirella</i>	—	2(2.2)	—	—	—	—	—	—	—	—	2(0.3)	
<i>Limnaeodius ocularis</i>	—	4(4.3)	—	1(1.9)	—	—	—	—	—	—	5(0.7)	
<i>Rana arcuata</i>	—	—	—	—	—	—	—	—	—	1(1.8)	1(0.1)	

Table 1. Continued

Species	River swamp	Longleaf flatwoods	Slash flatwoods	Pond pine	Hydric hammock	Mexic hammock	Xeric hammock	Longleaf sandhills	Turkey oak sandhills	Sand pine scrub	Rosemary scrub	Total all sites
<i>R. catesbeiana</i>	—	—	—	—	—	2(4.3)	—	—	—	—	—	2(0.3)
<i>R. clamitans</i>	—	—	—	—	2(3.8)	—	2(5.1)	—	—	—	—	4(0.5)
<i>R. gryllus</i>	—	—	—	—	—	1(2.2)	—	—	—	—	1(1.8)	2(0.3)
<i>R. heckscheri</i>	3(20.8)	—	—	—	—	—	—	—	—	—	—	3(0.4)
<i>R. sphenocephala</i>	—	2(2.2)	—	—	4(7.6)	16(34.5)	—	—	—	—	2(3.7)	24(3.2)
<i>Stilosoma extenuatum</i>	—	—	—	—	—	—	—	—	1(0.9)	—	1(1.8)	2(0.3)
<i>Tamilla relicta</i>	—	—	—	—	—	—	5(13.0)	27(36.6)	17(15.5)	20(18.6)	11(20.1)	80(10.7)
<i>Thamnophis sirtalis</i>	—	1(1.1)	1(3.4)	—	2(3.8)	—	—	3(4.1)	—	—	—	7(0.9)
<i>Skistronus millarius</i>	—	—	—	—	1(1.9)	—	—	2(2.7)	1(0.9)	—	—	4(0.5)
<i>Ameiurus fulvius</i>	—	—	—	—	—	—	—	2(2.7)	—	1(0.9)	—	3(0.4)
Total Species	3	16	7	6	17	12	10	13	16	19	21	43
Total Individuals ^a	7(48.6)	116(135.5)	21(72.2)	29(174.7)	120(229.0)	99(213.3)	59(151.3)	162(219.5)	118(107.7)	147(136.5)	87(159.3)	965(129.8)
Shannon-Wiener Index ^a	1.00	2.10	1.04	1.32	2.01	1.98	2.04	1.97	2.21	2.22	2.46	2.61

^a*Eleutherodactylus* has been omitted from these calculations. See text.

habitats. Two arrays were constructed without drift fences and funnel traps, but were otherwise identical to the standard. These were ineffective, taking only an occasional specimen of *Sceloporus undulatus* and *Cnemidophorus sexlineatus*.

In another experiment we set up a continuous 30-m tarpaper drift fence with eight buckets and eight funnel traps, representing the same length and number of traps as a standard array. This system proved only marginally effective, primarily because the tarpaper fence had a tendency to droop in the summer heat and required almost daily maintenance.

We also installed six sets of 3-m-long pressure-treated boards with a jar-funnel trap on each end as described by Clark (1966). Although these traps proved effective for Clark in Kansas, they collected only a single specimen of *Gastrophryne* in Ocala. The 3-m board may not be a long enough fence to interrupt animal movements in the open Florida sandhills and scrub habitats, and their low (12- to 14-cm) height may not effectively divert some species.

Quadrat Method

Sampling amphibians and reptiles by attempting to collect all individuals in a specified quadrat has been used in previous herpetofaunal surveys (e.g., Lloyd et al. 1968; Heyer and Berven 1973; Scott 1976 and this volume; Inger and Colwell 1977). We tested this technique during the study at four of the same sites where our herp arrays were already operating, but at a minimum of 500 m away from the arrays. Three replicates were performed in each habitat type, one each in the spring, summer, and autumn. Quadrats of 1,000 m² were marked off with nylon string and searched by a team of three or four experienced field herpetologists. Larger and more active species were noted as they dispersed off the quadrat. Several passes were then made through the marked area removing surface litter and inspecting all possible retreats. An average of 6 man-hours was required to reach the point where we felt additional collecting would yield no more specimens.

Time-constrained Technique

We used the same four sites to test the method

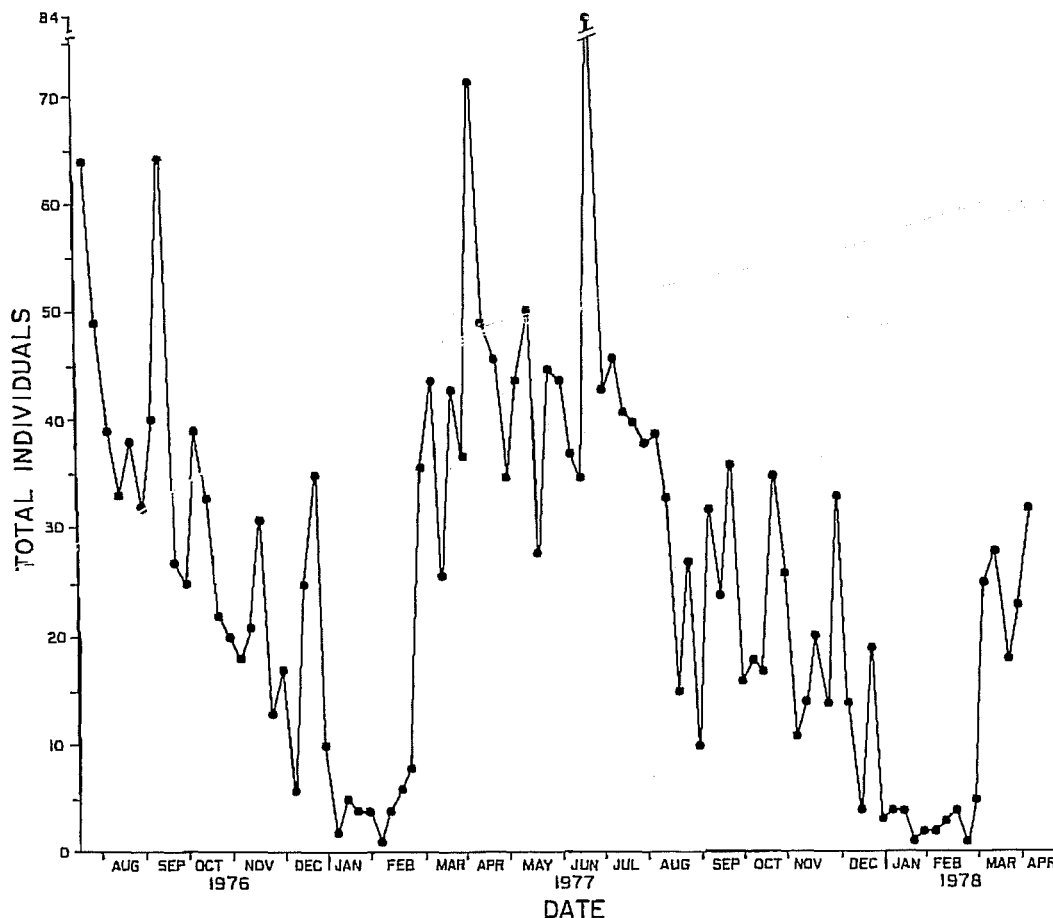


Fig. 4. Total individuals trapped by date at six sites (12 arrays) in sand pine scrub in the Ocala National Forest, Florida. Trapping effort was equal at each site.

of general herpetological collecting per unit time. There were no boundaries except that the collectors remained inside the specific habitat and at least 500 m away from the arrays and 1,000-m² quadrats. Experienced field herpetologists moved through the habitat turning logs, inspecting retreats, and watching for surface-active amphibians and reptiles. Three 6-man-hour replicates were performed in each habitat type, one each in the spring, summer, and autumn.

Comparison of Quantitative Techniques

Inspection of Table 2 shows that in the sand-hill and scrub habitats, the array system yielded

the maximum returns for approximately equal effort expended. Both of these habitat types are dominated by pine trees which offer little cover for amphibians and reptiles. However, in the flatwoods and hammocks, cabbage palm (*Sabal palmetto*) and several broadleafed scrubs and trees provide hiding places for treefrogs that are not usually collected by the arrays. Small wet areas in both flatwoods and hammock sites provide additional microhabitat for species not normally encountered in the drier sandhills and scrub.

Nocturnal Road Cruising

Road cruising or night driving is a well-known technique involving driving a vehicle at

Table 2. Total numbers of individuals and species collected at four sites (slash pine flatwoods, xeric hammock, turkey oak sandhills, and sand pine scrub) along the route of the proposed Cross Florida Barge Canal by three sampling techniques.

Habitat type	Quadrat		Time-constrained		Array	
	No.	Species	No.	Species	No.	Species
Slash pine flatwoods	30	9	31	14	110	7
Xeric hammock	39	6	106	18	59	10
Turkey oak sandhills	30	6	75	13	119	16
Sand pine scrub	23	8	48	10	148	19
Total	122	15	260	24	436	29

Table 3. Amphibian and reptile species collected during the Cross Florida Barge Canal Wildlife Restudy by three sampling techniques at four sites (slash pine flatwoods, xeric hammock, turkey oak sandhills, and sand pine scrub) and by nocturnal road cruising through a wider variety of habitats. R = road cruising, Q = quadrats, TC = time-constrained, A = array system.

Species	R	Q	TC	A	Species	R	Q	TC	A
<i>Notophthalmus viridescens</i>			x		<i>E. inexpectatus</i>		x	x	x
<i>Plethodon glutinosus</i>			x		<i>E. laticeps</i>				x
<i>Scaphiopus holbrooki</i>	x			x	<i>Scincella laterale</i>		x	x	x
<i>Gastrophryne carolinensis</i>	x	x	x	x	<i>Cemophora coccinea</i>				x
<i>Bufo quercicus</i>	x			x	<i>Coluber constrictor</i>	x		x	x
<i>B. terrestris</i>	x	x	x	x	<i>Diadophis punctatus</i>	x			x
<i>Acris gryllus</i>					<i>Elaphe guttata</i>	x			
<i>Hyla chrysoscelis</i>	x				<i>E. obsoleta</i>	x			
<i>H. cinerea</i>	x		x		<i>Farancia abacura</i>	x			
<i>H. crucifer</i>	x	x	x		<i>F. erythrogramma</i>	x			
<i>H. femoralis</i>		x	x		<i>Heterodon simus</i>				x
<i>H. gratiosa</i>	x		x	x	<i>Lampropeltis getulus</i>	x			
<i>H. squirella</i>	x	x	x		<i>L. triangulum</i>	x			
<i>Limnaeodex ocularis</i>		x	x		<i>Masticophis flagellum</i>	x		x	x
<i>Pseudacris nigrita</i>	x				<i>Nerodia fasciata</i>	x			
<i>P. ornata</i>	x				<i>Ophedrys aestivus</i>	x	x		
<i>Rana areolata</i>	x			x	<i>Pituophis melanoleucus</i>				x
<i>R. catesbeiana</i>	x				<i>Regina rigida</i>	x			
<i>R. gryllis</i>					<i>Rhadinea flavilata</i>		x		
<i>R. heckscheri</i>	x				<i>Seminatrix pygaea</i>	x			
<i>R. sphenocephala</i>	x		x		<i>Stilosoma extenuatum</i>	x			x
<i>Eleutherodactylus planirostris</i>			x	x	<i>Storeria dekayi</i>	x			
<i>Kinosternon bauri</i>	x	x		x	<i>Tantilla relicta</i>		x	x	x
<i>Cophorus polyphemus</i>		x	x		<i>Thamnophis sauritus</i>	x			
<i>Rhineura floridana</i>			x	x	<i>T. sirtalis</i>	x			x
<i>Anolis carolinensis</i>		x	x	x	<i>Micrurus fulvius</i>	x			x
<i>Sceloporus undulatus</i>			x	x	<i>Agkistrodon piscivorus</i>	x			
<i>S. woodi</i>			x	x	<i>Crotalus adamanteus</i>	x			
<i>Cnemidophorus sexlineatus</i>			x	x	<i>Sistrurus miliarius</i>	x		x	x
<i>Ophisaurus ventralis</i>	x			x					
<i>Enemecus egregius</i>	x			x	Total	38	15	24	29

Table 4. Amphibian and reptile species collected only by generalized herpetological collecting during the Cross Florida Barge Canal Wildlife Restudy.

<i>Siren intermedia</i>	<i>C. nelsoni</i>
<i>S. lacertina</i>	<i>C. scripta</i>
<i>Pseudobranchius striatus</i>	<i>Deirochelys reticularia</i>
<i>Ambystoma talpoideum</i>	<i>Malaclemys terrapin</i>
<i>Desmognathus auriculatus</i>	<i>Terrapene carolina</i>
<i>Eurycea quadridigitata</i>	<i>Trionyx ferox</i>
<i>Amphiuma means</i>	<i>Ophisaurus attenuatus</i>
<i>Chelydra osceola</i>	<i>O. compressus</i>
<i>Kinosternon subrubrum</i>	<i>Eumeces fasciatus</i>
<i>Sternotherus minor</i>	<i>Drymarchon corais</i>
<i>S. odoratus</i>	<i>Heterodon platyrhinos</i>
<i>Chrysemys concinna</i>	<i>Nerodia taxispilata</i>
<i>C. floridana</i>	

40-50 km/h along secondary roads. Low headlight beams are effective in revealing amphibians and reptiles as they cross the road (Klauber 1939). This technique often yields data not otherwise obtainable without unreasonable commitment of time and manpower, especially where secondary, hard-surfaced roads run through habitats of interest. During the Barge Canal study, we recorded 38 species of amphibians and reptiles in 2,903 km of nocturnal road driving. The list includes a number of rare species (*Hyla chrysoscelis*, *Rana areolata*, and *Stilosoma extenuatum*) and three species not otherwise collected during the study: *Farancia erytrogramma*, *Regina rigida*, and *Nerodia fasciata*. Table 3 lists the species collected by this technique and provides a comparison with the other sampling techniques.

Opportunistic Collecting

The four sampling methods allowed us to determine much of the regional herpetofauna, but there were still an additional 25 species that were only opportunistically located during general field activities (Table 4). Thus, although the standardized trapping program, combined with specific activities such as road cruising, quadrat collecting, and time-constrained sampling periods, is effective in providing data on relative abundance of species, seasonal abundance, and relative diversity in different habitats, it does not fully replace the snake collector with potato rake and cloth sack if maximum information on

faunal composition is one of the objects of a survey.

Acknowledgments

Our past and present studies of herpetological communities would have been much less successful without the enthusiastic support of numerous individuals; C. R. Smith, H. I. Kochman, and W. S. Lippincott deserve special mention.

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Evaluation of Techniques for Assessment of Amphibian and Reptile Populations in Wisconsin

by

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Abstract

This study was part of a project to develop techniques for sampling terrestrial vertebrates quantitatively and qualitatively by nonspecialized biologists. Drift fences combined with traps proved to be a practical way to uniformly census reptiles and amphibians. Drift fences made from aluminum valley caught more animals per 15 m of fence than those made of either screening or galvanized metal. Aluminum valley is easy to handle and stands up well with continued use. Generally, the more fence set, the more animals caught. Fences shorter than 15 m, however, did not catch enough animals to make their use worthwhile. A height of 50 cm proved effective. A system of 18.9-L traps, 7.6-L traps with funnel rims, and funnel traps were necessary to capture the entire spectrum of amphibians and reptiles in the communities sampled. We believe that several short sampling periods staggered throughout the season are more effective in obtaining an estimate of species composition and populations than a longer sampling period at any one time. Procedures are recommended for using drift fences and traps in various habitats.

Reptiles and amphibians are sometimes difficult to census, as they may remain inactive for weeks if weather conditions are not within their activity range. Temperature, precipitation, soil moisture, humidity, light intensity, wind, and season greatly control their activity patterns. Thus, any census technique must take into consideration the effects of these factors on the animals' biology.

The present study was part of a project to develop techniques for sampling terrestrial vertebrates quantitatively and qualitatively by a nonspecialized biologist. The emphasis was on a

uniform sampling method that could be applied to the Till Plain of the northern United States, while maximizing efficiency without losing accuracy.

A number of sampling methods have been used to determine species density and diversity of amphibians and reptiles. Most environmental impact statements give species lists of reptiles and amphibians seen or captured through random search and seize procedures. The success of the techniques varies greatly with the training of the individuals involved, the time of the day and year the collecting is done, the rareness or agility of a species, and the type of habitats sampled. Though fast-moving or secretive species may actually be fairly common, they may not be found if the observer is not looking in the right place. For example, in this study, over 50 h were spent

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looking for reptiles and amphibians over a 5-year period at the Portage site, but not until drift fences were employed did *Ophisaurus* appear in the sample. Different species vary in their daily and seasonal activity patterns; thus an observer might notice few salamanders above ground on bright, sunny days, no lizards active during a rain, or snakes active on cloudy, windy days. The long-term use of an area must also be considered if habitat has to be destroyed while searching for specimens.

Population estimates and other quantitative comparisons require extensive search and capture, and often marking. The time of sampling and training of observers are also important. The animals must be marked so that individuals are not counted more than once unless the animals are removed from the population. Salamanders, lizards, frogs, and turtles can all be easily toe-clipped for short-term marking, and snakes can be scale-clipped (Blanchard and Finster 1933; Martof 1953).

Call indices for frogs are of limited use; only mature male frogs call, and in many species only dominant males call. A pond with 18 calling males may have an additional 64 mature subdominants, or may have none, but the population estimate would be the same (Fellers 1975). A call index is, however, a good estimate of the size of the breeding area—the more widespread the calling males, the larger the breeding area. Difficulty in estimating the number of nonterritorial frogs or frogs with very small territories must also be considered. *Hyla crucifer* and *Rana sylvatica* often call in dense choruses numbering in the hundreds. Separating the individual calls is nearly impossible, except possibly by taping and computer analysis.

Frogs are also highly seasonal, and calling is affected by temperature and time of day (see Wiest, this volume). Though only a few frogs may be heard early and late in the season, hundreds may be calling at the peak of the breeding season. In Wisconsin, *Rana sylvatica* calls for only a 2-week interval in early spring. At this time, only *Pseudacris* and *H. crucifer* are also calling. Later in the season *Pseudacris*, *H. crucifer*, *H. versicolor*, and *Bufo* may all be heard calling in the same area, while *Acris* and *R. clamitans* have yet to start. A sampling period would need to cover the entire range of breeding time and on nights of proper temperature and moisture for each species. Its value as a census

technique is generally limited to data on species presence. Call differences, however, are the surest way for the nonspecialist to differentiate some species of frogs (e.g., *Hyla chrysoscelis* from *H. versicolor*, or *Rana blairi* from *R. pipiens*).

Fitch (1951) described using funnel traps with and without doors for capturing snakes, lizards, and frogs. He was interested in population dynamics of snakes and set the traps along natural drift fences, e.g., logs and rock ledges. This was an effective method for capturing animals moving along these areas, but choosing such areas requires knowledge of the types of animals being studied. Funnel traps with drift fences were also found to be highly effective by Imler (1945) for bull snakes (*Pituophis*); 1,729 were caught in four summers. Milstead (1959) used drift fences with funnel traps for catching lizards in Texas. Campbell and Christman (this volume) have used funnel traps effectively.

Pit traps of various depths and diameters with and without drift fences have been used in various studies. Covered pit traps are effective in catching lizards (Banta 1957; Lillywhite 1977). Moreover, when they are employed with a drift fence, results have often been exceptional (Shoop 1968; Gibbons and Bennett 1974; Rittschof 1975; B. Hellmich, personal communication; D. Tinkle, personal communication; Campbell and Christman, this volume). Drift fencing seems to be the most effective method of reducing inherent observer bias.

D. Tinkle (personal communication) walked along drift fences and counted animals that came up to the barrier and were trying to move around it. This is satisfactory for long (over 100 m) permanent fences that are irregularly monitored. Short fences (less than 100 m) need restraining devices such as pit and funnel traps associated with them to be effective.

Although drift fences and traps are more cumbersome and expensive than walking a line transect or searching a quadrat, these drawbacks are more than compensated by the elimination of the observer and temporal biases. Because of its effectiveness and efficiency, the drift fence and trap method seem the best way to standardize sampling of reptile and amphibian communities.

The present study, undertaken from April through November 1976, was devised to test different aspects of drift fences with pits and fun-

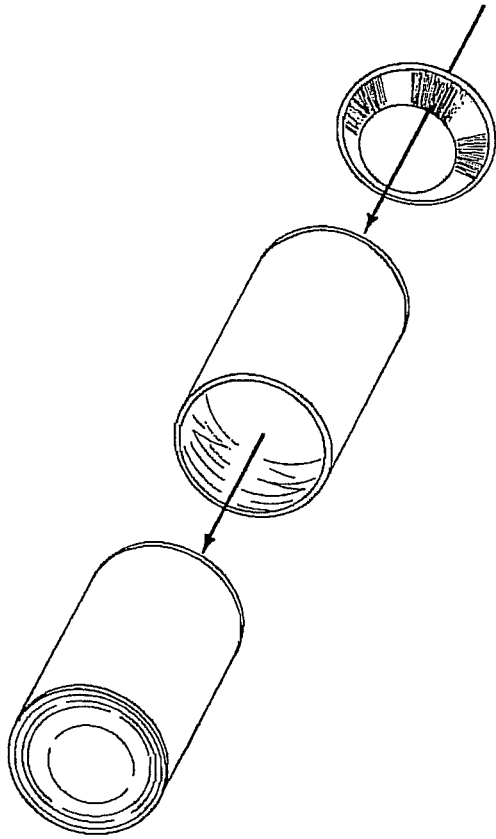


Fig. 1. Construction of a 7.6-L pit trap with funnel.

nels. The materials, length, height, and positioning of fence, the size and type of pits and funnel traps, the season and weather, and the length of time needed to sample were tested to formulate a standardized method.

Materials and Methods

The sampling unit is defined here as the length of the drift fence. In the text, drift fence refers to either the fence alone or the drift fence with its associated traps. The exact meaning should be clear from the context.

The following materials were tested for fencing and traps: aluminum valley (or flashing), 15-m roll, 50 cm high; aluminum window screen, 15-m roll, 60 cm high; galvanized sheet metal, 3 m by 60 cm; 3.8-L cans with funnel rims; 7.6-L cans made by cutting the bottom out

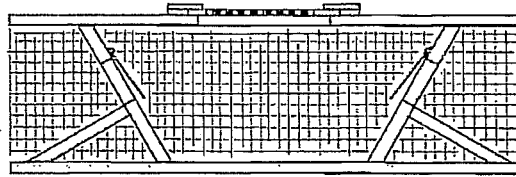


Fig. 2. Funnel trap (after Fitch 1951).



Fig. 3. Drift fence made from aluminum valley. Note bend in fence around a rock (Point Beach, Line A).

of one can and securing two cans together with 7.5 cm duct tape (Fig. 1); plastic bowls with bottoms removed for attachment to 3.8-L and 7.6-L cans as funnel rims (Fig. 1) and bowl lids; 18.9-L plastic ice cream buckets with lids; 18.9-L metal paint cans with lids; and two-door funnel traps (Fig. 2).

Drift fences made from the aluminum valley were set up in either 15 or 30-m lengths in a 10-cm trench (Fig. 3) with a galvanized metal stake set at each end of the valley. The aluminum screen was set in 7.5 to 30-m lengths, buried 10 cm underground, and staked with wood lathe every 2 m. The galvanized metal sheets were fastened together, buried 15 cm underground, and staked with galvanized angle iron between each sheet (Fig. 4).

A combination of funnel traps and the following types of pit traps were used: 3.8-L cans with and without funnel rims, 7.6-L cans with and without funnel rims, and 18.9-L buckets. Traps were set at various distances along the fence. Pit traps were buried flush with the surface of the soil, and funnel traps were set against the fence and tight against the soil. Traps were checked at least every other day, and all animals were marked and released 3 m on the opposite

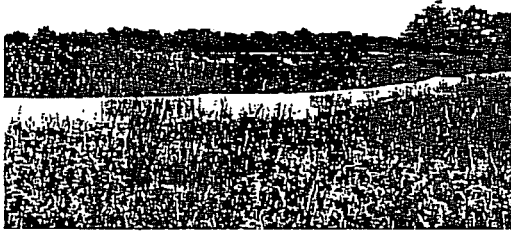


Fig. 4. Drift fence made from galvanized metal (Blue River, Line 1).

side of the fence. If weather conditions were not right, covers were placed on pit and funnel traps until the weather became more suitable.

Test trap lines were set up with the same number of each type of trap on both sides of the fence. The low number of animals caught did not warrant the rotation of trap positions. All trapping of reptiles and amphibians was conducted in 1976 unless otherwise designated. Scientific and common names for reptiles and amphibians encountered in the study are listed in the Appendix.

Study Areas

Three main habitat types were used for testing various aspects of drift fencing in southern Wisconsin: oak-hickory woodlots, wetlands, and old fields and prairie. A short period of trapping was also conducted in mixed deciduous forest.

Oak-Hickory Woodlots

These areas were chosen to compare results of reptile and amphibian sampling in an area where small mammals, birds, and vegetation were also being censused. Small deciduous woodlots in southern Wisconsin are not notably productive of a high diversity of reptiles or amphibians. The effectiveness of 3.8-L vs. 7.6-L pits and the position bias of the fence were tested at these sites. Traps were open for 24 days, between 27 April and 21 May.

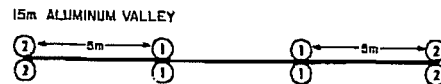
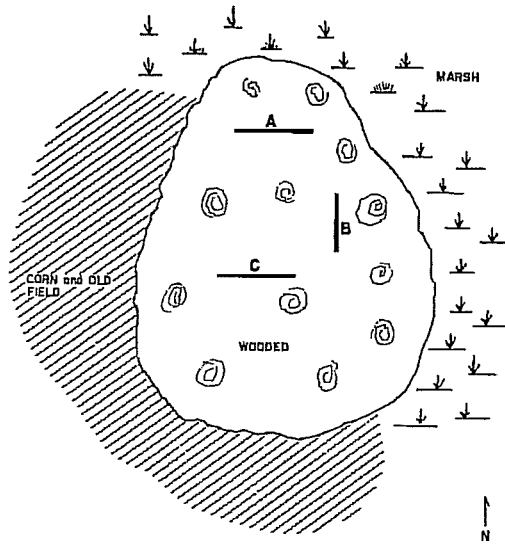


Fig. 5. Shaw Marsh site, Wisconsin. All three lines were constructed in a similar fashion. The symbols 1 and 2 refer to the positions of 3.8 and 7.6-L pit traps.

Shaw Marsh Woodlot, Dodge County (T11N R14E, Sec 22 NW 1/4)

This oak-hickory forest (Fig. 5) had a mean of 245 trees (≥ 10 cm diameter) and 746 saplings per ha. There was a dense herbaceous understory with many fallen logs, mostly elm, which provided excellent cover for woodland amphibians and reptiles. The forest was bordered by a cattail marsh and an intermittent stream on the north and east. To the south and west it was bordered by cornfields and an old field.

Busse Tract, Columbia County (T12N R12E, Sec 22 SW 1/4)

This oak-hickory woodlot (Fig. 6) had a mean of 264 trees and 469 saplings per ha. A small irrigation ditch and canary grass field were to the west and north of the woods. A young (6 to 8 years) pine plantation was on the east and a cornfield on the south.

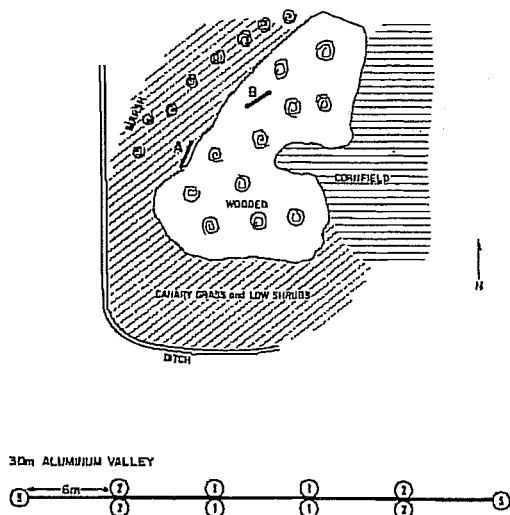


Fig. 6. Busse Tract site, Wisconsin. Both lines were constructed in a similar fashion. The symbols 1, 2, and 5 refer to the positions of 3.8, 7.6, and 18.9-L pit traps.

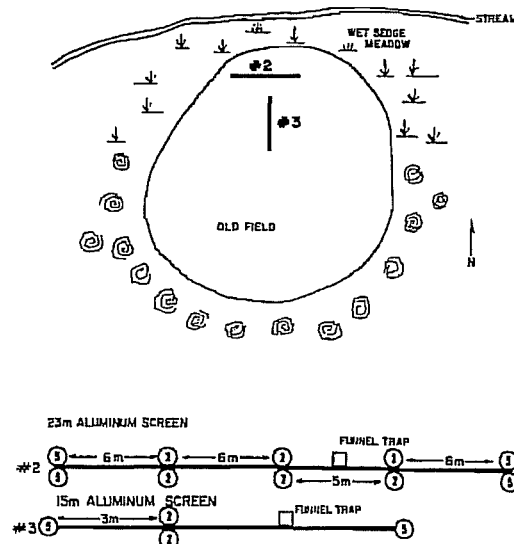


Fig. 7. Portage A site, Wisconsin. The symbols 2 and 5 refer to the positions of 7.6 and 18.9-L pit traps.

Wetlands and Old Fields

Portage site, Columbia County (T12N R9E, Sec 28, 33; T11N R9E, Sec 4)

Drift fences and traps were set in three old fields adjacent to wetlands and around a woodland pond. All four sites were on the land of Wisconsin Power and Light Coal Generating Plant, south of Portage. Traps were monitored from 22 April to 3 November. These lines were set to test position bias, effectiveness of trap types, and length and type of fence.

North Knoll—old field along Duck Creek (Fig. 7).—The area was bordered by a lowland hardwood forest to the south and sedge meadow to the north. During the spring, the sedge meadow is flooded by Duck Creek.

North Knoll—adjacent to the Intake Channel (Fig. 8).—This area was an old field adjacent to a short strip of marsh about 50 m wide, adjacent to the intake channel from Duck Creek to the Power Plant. It was bordered on the east and west by lowland hardwood forest and to the south by a large sand blow which was used for nesting by turtles.

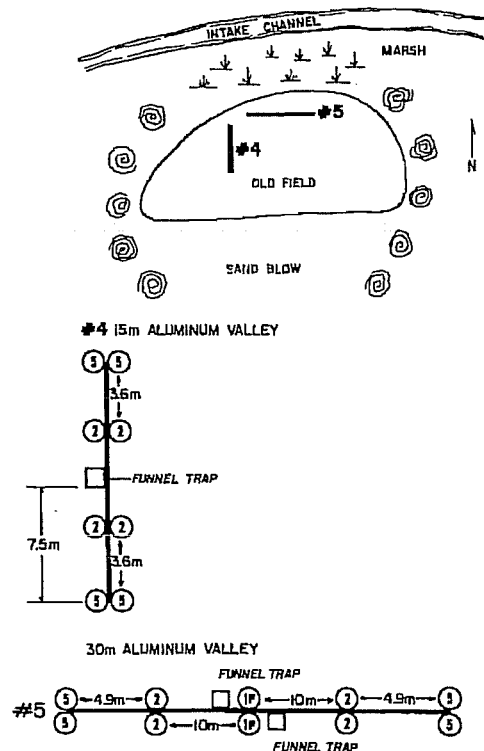


Fig. 8. Portage B site, Wisconsin. The symbols 2, 5, and 1F refer to the positions of 7.6 and 18.9-L pit traps and 3.8-L pit traps with funnels.

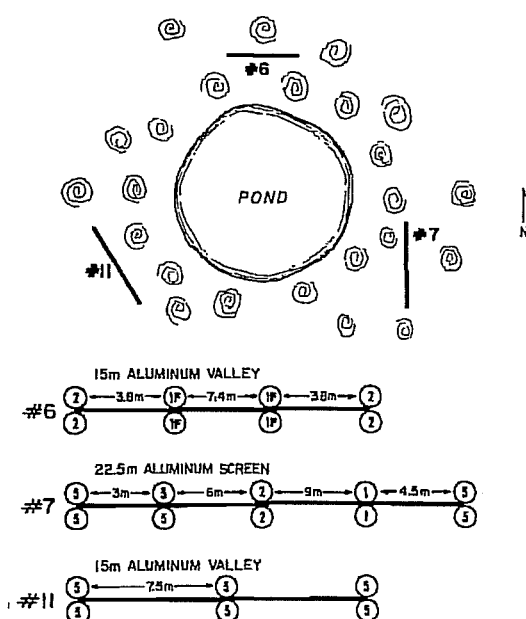


Fig. 9. Portage C site, Wisconsin. The symbols 1, 2, 5, and 1F refer to the positions of 3.8, 7.6, and 18.9-L pit traps and 3.8-L pit traps with funnels.

North Knoll—Woodland Pond (Fig. 9).—Three pieces of fencing were installed on the north, east, and west sides of a woodland pond, 3 m from the shore. The pond was about 30 × 30 m and 1.5 m deep, surrounded by a young oak, hickory, and paper birch woods.

South Knoll (Fig. 10).—This site was in an old field on clay soil adjacent to a small cattail marsh to the north and a lowland hardwood forest to the west. The east and south borders of the field were bordered by the settling pond and overflow channel.

Long Lake, Manitowoc county, (T19N R21E, Sec 6)

The northeast edge of the lake was bordered by a cattail marsh and an alfalfa field upland from the cattails (Fig. 11). This area was chosen to test the efficiency of drift fences versus hand capture. Between 1 April and 10 September, 200 man-hours were spent by another researcher marking frogs in the area. Because of dry soil conditions, the two 15-m aluminum drift fences were set 5 m from the alfalfa field in the marsh,

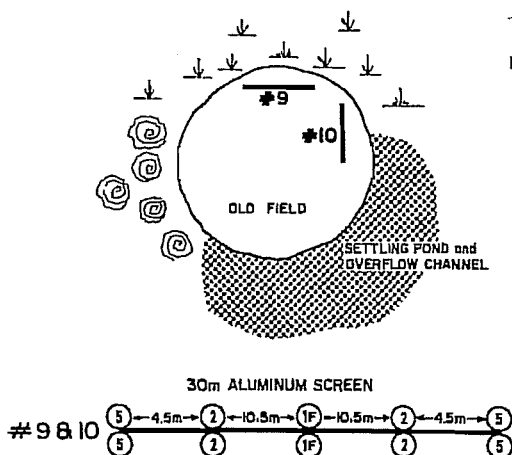


Fig. 10. Portage D site, Wisconsin. The symbols 2, 5, and 1F refer to the positions of 7.6 and 18.9-L pit traps and 3.8-L pit traps with funnels.

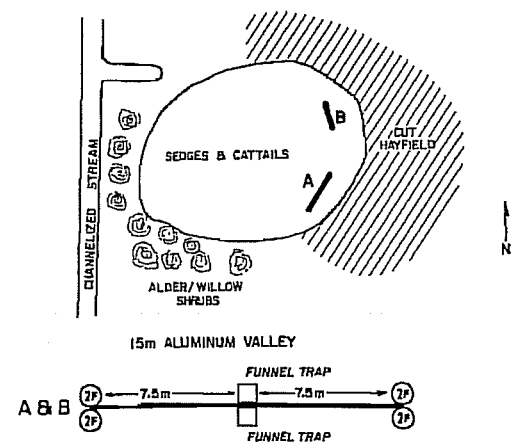


Fig. 11. Long Lake site, Wisconsin. The symbols 2 F refer to the positions of 7.6-L pit traps with funnels.

and traps were open for 12 days in September and October.

Prairie

Blue River Cactus and Dunes, Grant County, (T8N R1W, Sec 6 E 1/2)

This 52.6-ha area featured a variety of xeric plant community types including sand blows, active dunes, flat sand barrens, and stabilized dunes forested with oaks (Fig. 12). *Hudsonia* is

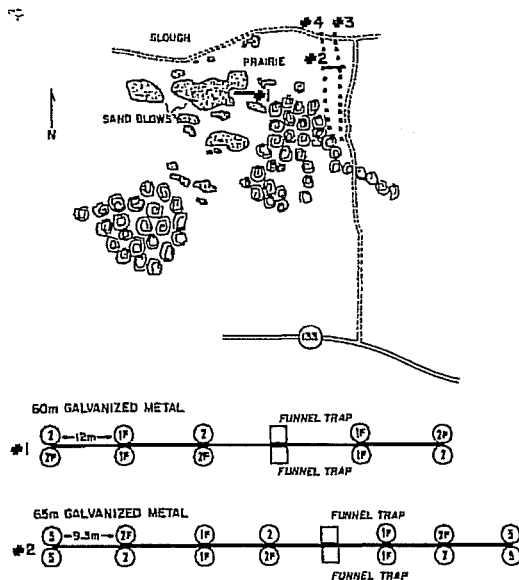


Fig. 12. Blue River site, Wisconsin. The symbols 2, 5, 1F, and 2F refer to the positions of 7.6 and 18.9-L pit traps and 3.8 and 7.6-L pit traps with funnels.

abundant; other dune binders include *Arctostaphylos*, *Selaginella*, fungi (*Geaster*), mosses, and green algae. Two succulents, *Talinum rugospermum* and *Opuntia compressa*, occurred here. Nearly 12 ha were forested with oaks, often with an understory dominated by *Carex*. The soil type was Sparta loamy fine sand. It is almost certain that the area was once cultivated; subsequent wind erosion and loss of fine soil particles resulted in abandonment of the land.

Two fence and trap systems were set (Fig. 12). Line No. 1 was near the southeast end of a large sand blow (Fig. 4). Line No. 2 was in the northeast corner of the area in the center of the sand prairie and 3 m from the dirt road at the boundary. The traps were open for 85 days, between 26 May and 25 August.

Ten funnel traps, facing north-south, were set 20 m apart in a transect perpendicular to the center of drift fence No. 2 (position No. 3 on Fig. 12). After two weeks, the transect was moved to the west edge of drift fence No. 2 (position No. 4 on Fig. 12). These transects were run to determine the feasibility of using funnel traps without drift fences and also to see how far individual lizards moved within the study area.

Spring Green Reserve, Sauk County (T8N R4E, Sec 5, 6)

This area consisted of 113.3 ha of sand bar-

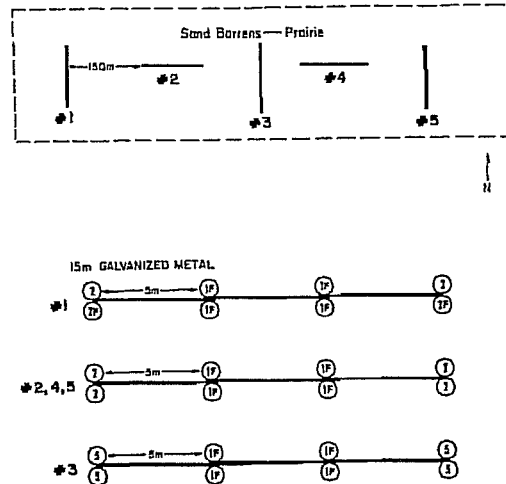


Fig. 13. Spring Green site, Wisconsin. The symbols 2, 5, 1F, and 2F refer to the positions of 7.6 and 18.9-L pit traps and 3.8 and 7.6-L pit traps with funnels.

rens—prairie and old fields bordered by a dry-line prairie and a southern dry-mesic forest on the hills on the northern boundary, with crop lands on the east, south, and west borders (Fig. 13). There was no temporary or permanent water or wetlands within a 2½-km radius. Position of fence, type of trap, and movement of animals were being tested at this site. Relative numbers of each species were known from work over the previous 15 years by one of us (RCV). Three species of lizards, seven species of snakes, and one species of turtle were known to inhabit this area. This area was chosen to test the trapping procedure on an area of high species diversity and known species composition.

Mixed Deciduous Forest

Point Beach State Forest, Manitowoc County, (T20N R25E, Sec 29)

This area was a mixed deciduous forest with a dense canopy and thick understory of herbaceous plants and mulch (Fig. 14). The area was used to test the use of drift fences, as opposed to counting frogs in quadrats, and to check the reliability of drift fences in determining species composition. Three adjacent 9 × 9-m quadrats (1, 2, and 3, Fig. 14) and one separate quadrat (4, Fig. 14) were censused by another experienced investigator who walked back and forth counting frogs for 2.5 h.

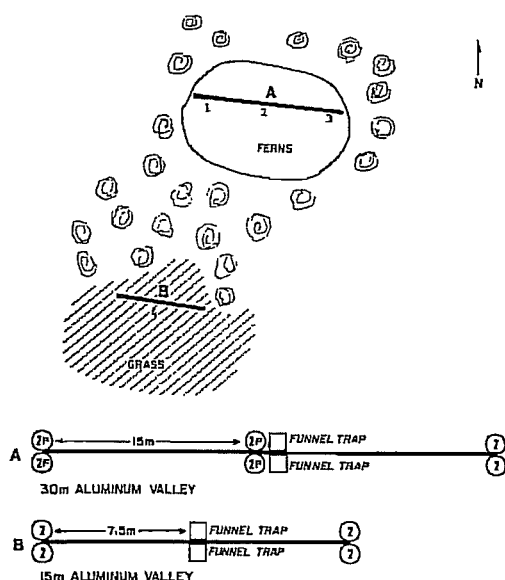


Fig. 14. Point Beach site, Wisconsin. The symbols 2 and 2F refer to the positions of 7.6-L pit traps and 7.6-L pit traps with funnels.

Evaluation of Drift Fence Trap Techniques

Effectiveness of Fencing Materials

The traditional measurement for animals caught in traps is number caught per trap day. Drift fences made from aluminum screening caught a slightly greater number of reptiles and

amphibians per trap-day than did fences made of either aluminum valley or galvanized metal (Table 1).

In testing the various fencing materials, however, the number of animals caught per trap-day was not the best measurement of effectiveness, since the number and size of pit traps associated with individual fence lines were variable. Therefore, the unit of measurement regarded as most reliable was number of animals caught per 15 m of fence (Table 1). This new measurement of effectiveness showed a slightly greater number of animals caught with drift fences made from aluminum valley than with aluminum screen (33 and 31 animals per 15 m of fence-day $\times 100$, respectively).

Fences caught all forms of reptiles and amphibians regardless of fencing material. A potential drawback to the screen is the ability of some animals to crawl over it. This may have happened with the salamanders—only six salamanders were caught in 120 m of screen, whereas 18 were caught in 7.5 m of aluminum. On three occasions, garter snakes were seen going over the screen fences, once without being pursued and twice when an observer was walking along the fence. The same size snakes were never seen going over the aluminum. The use of numerous stakes along the screen fence provided “ladders” for many small snakes, lizards, and salamanders to work their way over the fence. This was not a problem with aluminum. Galvanized metal used at Blue River was an effective barrier to all forms known to inhabit that prairie and caught animals at the rate of 12 animals per 15 m of fence-day $\times 100$ (Table 1).

Table 1. Numbers of animals caught with different drift fence materials in southern Wisconsin.

	Portage Area		Blue River Area
	Aluminum valley	Aluminum screen	Galvanized metal
Frogs and toads	154	228	—
Salamanders	18	6	—
Snakes and legless lizards	69	114	167
Turtles	15	11	—
Total	256	359	167
No. traps	35	46	28
No. trap days	5,198	6,550	4,760
Animals/trap day $\times 100$	4.9	5.4	3.5
No. 15-m lengths of fence	5	8	8
No. 15-m fence days	733	1,145	1,360
Animals/15-m fence-day $\times 100$	35	31	12

Evidence from trails in the sand showed no snakes or lizards going over the fence. However, these results are not directly comparable to the catch with the other two fence materials, because of the habitat differences of the study areas.

Screen weighs much less than the solid aluminum and is a little easier to carry; a roll of aluminum weighs about 9 kg and rolls into a cylinder 41 cm in diameter. It has nearly the same flexibility as screen for going around logs, trees, and rocks. Though aluminum needs a stake at each end only, screen requires staking at least every 3 m or the fence sags and animals crawl over it more easily. Aluminum stands up better over continued setting and pulling of fences; screen tends to tear and get matted with dirt and debris. The galvanized metal is excellent for a permanent fence, but there are disadvantages since the sheets weigh about 20 kg apiece and cannot be rolled and transported easily.

Length, Height, and Position of Fence

Fence lengths of 3-60 m were tested. Generally, the more fence set, the more animals caught. Drift fences shorter than 15 m, however, did not catch enough animals to make their use worthwhile.

A comparison of the catch along two pairs of 30-m and 15-m lengths of fence, set perpendicular to each other, was made in two old fields at Portage (Table 2). Twice as much fence resulted in the catch of about twice as many animals. Two 30-m sections set perpendicular to each other in a third old field caught comparable numbers of animals.

Since a fence must be high enough to discourage snakes from attempting to crawl over it or adult frogs from jumping over it, there is some optimum height needed to ensure the effectiveness of the fence and still maintain a manageable size. The minimum height used (50 cm) was sufficient to capture two 20-cm fox snakes, seven snakes over 40 cm, and hundreds of small snakes. Anything higher than this would be very unwieldy and is apparently not necessary for a census method.

There were often considerable differences in catch along various sections of fence within the same field and between adjacent fence lines. For example, at Portage (location No. 5) on 12 October, one 18.9-L pit trap caught 14 snakes, whereas the other 9 pit traps and 2 funnel traps

Table 2. *Comparison of numbers of animals caught in a 5-month period with 30-m and 15-m lengths of drift fence at the Portage site.*

	Lines 2 & 3		Line 4		Lines 9 & 10	
	30 m	15 m	30 m	15 m	30 m	15 m
Snakes	76	20	38	23	9	9
Turtles	7	2	4	0	1	1
Frogs and toads	90	83	49	22	20	14
Total	173	105	91	45	30	24
Animals/m	6	7	3	3	1	1.5

caught a total of only 5 snakes. Other differences in catch between fence lines in similar habitats are given in Table 3. Position of fence is especially important for migrating reptiles and amphibians. Fences set parallel to diverse habitat boundaries are more likely to pick up migrating animals than those set perpendicular to them, as animals are often moving across vegetation gradients (i.e., into or out of ponds, marshes, nesting grounds, and hibernacula). At Portage A, the northern marsh side of line 2 produced only 19 snakes, while the upland side had 48. However, line 3, set perpendicular to line 2, showed no difference in the number of snakes on either side of the fence (Fig. 7).

The catches of amphibians from the same fences, however, differed. Line 2 had no difference in the number caught on either side (40 vs. 49), but on line 3, 68 amphibians were caught

Table 3. *Differences between catches of selected groups of reptiles on different sampling lines in three similar habitats in southern Wisconsin.*

Location and group	Line number				
	1	2	3	4	5
Blue River					
<i>Elaphe culpinia</i>	4	0	—	—	—
<i>Heterodon</i>	3	0	—	—	—
<i>Chrysemys</i>	14	0	—	—	—
<i>Emydoidea</i>	7	0	—	—	—
<i>Cnemidophorus</i>	108	58	—	—	—
Portage					
<i>Ophisaurus</i>	—	—	—	2	0
Spring Green					
<i>Cnemidophorus</i>	10	0	0	2	13

on the east side and only 16 on the west side (29 of the 68 were *Rana pipiens* caught on a single day after a rain on 5 October). It is possible that the frogs were moving toward Duck Creek, a potential hibernaculum, which is on the west side of the fence.

At Portage B, line 5 showed no side bias for snakes or amphibians; line 4 had no side bias for snakes, but 18 of 21 amphibians were caught on the west side of the fence (Fig. 8). These examples show the importance of fixed migration patterns and the necessity for fences to be set as barriers in all directions to obtain the best sample.

Spring migrations of *Bufo* were obvious at both Shaw Marsh and Busse Tract. Catches at Shaw Marsh (Fig. 5) on 17 May indicated a definite movement towards the marsh. Thirty-four, 11, and 11 *Bufo* were caught on the sides of lines A, B, and C that faced away from the marsh, whereas 0, 6, and 5 were caught on sides nearest the marsh. The Busse woods (Fig. 6) showed the same phenomenon the same day—40 *Bufo* were caught on the eastern woods side of line A and 9 on the marsh side, and 19 *Bufo* were caught on the southeastern woods side of line B and 6 on the marsh side.

The Busse Tract also showed the desirability of placing several fences in different areas. On 9 July no amphibians were caught on line B in the woods, but 37 *Bufo* were caught on line A, all on the marsh side of the fence (all newly transformed young dispersing from the breeding ponds).

Types of Traps

Six different types of traps were set along drift fences to determine which were most effective and efficient (Table 4). Different kinds of reptiles and amphibians showed strikingly different responses to the various trap types.

Funnel traps were clearly more effective for catching lizards than pit traps. Of the pit traps, 18.9-L and 7.6-L traps with funnel rims were more effective than the 7.6-L traps without funnel rims (generally twice as many lizards caught) or 3.8-L traps with funnel rims.

Funnel traps were also effective for catching snakes. At Blue River, nine snakes, most over 40 cm, two over 1.2 m, were caught in funnel traps. Only one larger than 19 cm was caught in a pit trap. Similarly, in the Portage old field, all

seven snakes over 40 cm were caught in funnel traps. The 18.9-L cans were superior to the 7.6-L cans. The 3.8-L cans with funnel rims were also ineffective for snakes. Salamanders and frogs were rarely caught in funnel traps, but pitfalls were effective. Amphibians were caught in similar numbers in 7.6 and 18.9-L rimless pit traps, tested at the Portage sites. The 3.8-L cans with funnel rims caught a negligible number of amphibians. At the woodland pond site at Portage, the use of 3.8-L traps with funnel rims vs. 7.6-L traps without funnel rims was tested; the 7.6-L traps caught almost 10 times as many amphibians as the 3.8-L traps with funnel rims. Adult green frogs were observed at Blue River escaping from 7.6-L traps without funnel rims, but not out of the same sized traps with rims. However, 7.6-L traps without funnel rims worked well for juvenile frogs.

There was no difference in the catchability of frogs and toads between 3.8, 7.6, and 18.9-L pit traps, all without funnel rims, at the Busse Tract, but at Shaw Marsh there was a much higher catch in the 3.8-L traps. Although there were numerous tree frogs calling at Portage in the spring, very few were collected. This may be due in part to the location of the majority of fences outside the woods, or to the ability of the frogs with their adhesive feet to crawl readily over fences and out of pit traps.

The 18.9-L cans are necessary for capturing large adult turtles. Fifteen of the 21 adult turtles caught at Blue River were in the four 18.9-L buckets. Four turtles fell into the 12 7.6-L cans and 2 jammed their shells into the 3.8-L cans with funnel rims. Portage showed a similar pattern: 9 turtles in 30 18.9-L, 11 in 26 7.6-L, and 3 in 10 3.8-L traps. Hatchling turtles at both areas fell readily into any size pit. They were caught in both 7.6 and 3.8-L traps with funnel rims at Portage line No. 6.

In summary, 18.9-L pit traps are necessary for trapping adult turtles and are highly effective for small snakes and amphibians and lizards. The 7.6 and 18.9-L traps were effective for frogs and lizards, but the addition of the funnel rim on the 7.6-L traps (Blue River and Spring Green) appeared to yield an even higher catch. Funnel traps are best for lizards and are the only suitable trap for large snakes. The 3.8-L cans were unsuitable, except for some hatchling turtles and toads. A system of 18.9-L traps, 7.6-L traps with funnel rims, and funnel traps seems

Table 4. *Effectiveness of funnel traps and different sizes of pit traps set along drift fences for catching amphibians and reptiles. Animals caught expressed as number caught/trap day \times 100.*

Animal group and area	Pit Traps					Funnel traps
	3.8 L	3.8 L (with funnel rims)	7.6 L	7.6 L (with funnel rims)	18.9 L	
Lizards						
<i>Blue River</i> (340-680 trap days)	—	4.5	3.1	7.2	6.5	16.4
<i>Spring Green</i> (80-800 trap days)	—	0.8	1.9	7.5	0	5.4
Snakes and Legless Lizards						
<i>Portage</i> (540-3,780 trap days)	—	0.3	0.6	—	4.6	2.4
<i>Blue River</i> (340-680 trap days)	—	0	0	0	0.2	2.6
Frogs and Toads						
<i>Blue River</i> (340-680 trap days)	—	0	0.5	2.1	1.7	0.2
<i>Portage</i> (540-3,780 trap days)	—	0.4	3.0	—	3.3	0.6
<i>Shaw Marsh</i> (288 trap days)	23.0	—	9.7	—	—	—
<i>Busse Tract</i> (96-192 trap days)	33.3	—	29.2	—	30.2	—
Salamanders						
<i>Portage</i> (540-3,780 trap days)	—	0.3	0.2	—	0.1	0.4
Turtles						
<i>Portage</i> (540-3,780 trap days)	—	0	0.2	—	0.3	0
<i>Blue River</i> (340-680 trap days)	—	0.3	0.8	0	4.4	0

necessary to capture the spectrum of amphibians and reptiles in a community, although tree frogs were not adequately sampled by any of our methods.

Effect of Weather and Season

Precipitation markedly affects the activity of amphibians and reptiles. In 1976, Wisconsin experienced the worst drought in 40 years. When there was rain, amphibians moved immediately (Fig. 15). For example, before the rain, 0-5 animals were caught per 2-day interval at Portage, and 1-2 at Busse Tract and Shaw Marsh. On 15-16 May, 3.8 cm of rain fell; the response was 12 animals at Portage (Fig. 15), 69 at Busse, and 67 at Shaw. At Point Beach on 4 October, 18 frogs and 1 salamander were caught; after

1.1 cm of rain on 5 October, 257 frogs and 7 salamanders were caught within 24 h. Similar responses to rain were noted at Blue River (Fig. 15).

Lizards and snakes, unlike amphibians, often moved about 2 to 3 days after precipitation, whenever temperatures rose. The 5 October rain at Portage produced 97 amphibians and reptiles (mostly frogs), but on 12 October, several days after the rain, the temperature rose and 38 snakes were caught.

Both rain and temperature affected not only estimates of the presence of species, but also determinations of population levels (26 June-5 July). The movement of lizards at Blue River was highly erratic, due primarily to the summer weather conditions. Drought and high temperatures forced lizards to remain underground for

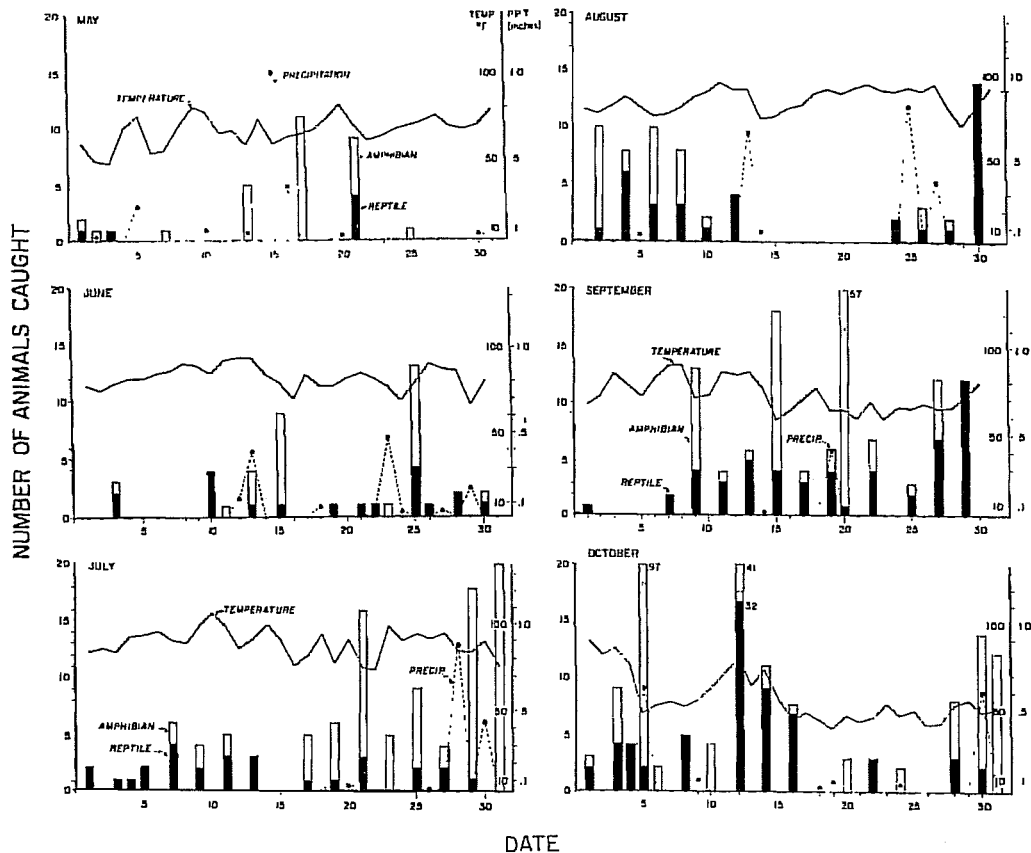


Fig. 15. Relation between catch of all reptiles and amphibians at Portage, Wisconsin, and precipitation and temperature.

days; after a rain, however, there was much more activity than normal, resulting in high population estimates (Fig. 16). A 4-day sample gave as accurate a population estimate as a 15-day sample. Normally, individual *Cnemidophorus* are active for a day or two of feeding, then retreat underground for a couple of days.

Spring and fall dispersal and migrations are also responsible for increased activity. At Blue River in mid-August there was an abrupt rise in the catch of lizards (Fig. 16). Most of these were hatchlings just emerging. Although the adults became inactive for the year at this time, the young remained active until mid-September.

Post-metamorphic migrations of toads were seen on the Busse Tract in early July, when 38 toads were caught along one side of a drift fence in one night. All were newly transformed and dispersing from the breeding ponds. The same phenomenon was observed at Portage in late

August, when the large number of snakes caught were mostly young of the year, presumably wandering away from their place of birth.

Amphibians and reptiles move to winter hibernacula in September and October. At Portage, more animals were caught in the fall following rain than in summer under similar conditions. In August and September, hatchling turtles were caught moving from the nesting sites to water.

Many species of salamanders spend most of their time underground or under cover, and their presence is usually known only during dispersal or migration times. This was apparent at Portage, where the only two *Ambystoma ligrinum* recorded were caught in late fall. Turtles caught at Portage and Blue River were aquatic, but females must come to land to lay eggs from late May to early July.

High numbers of amphibians and reptiles

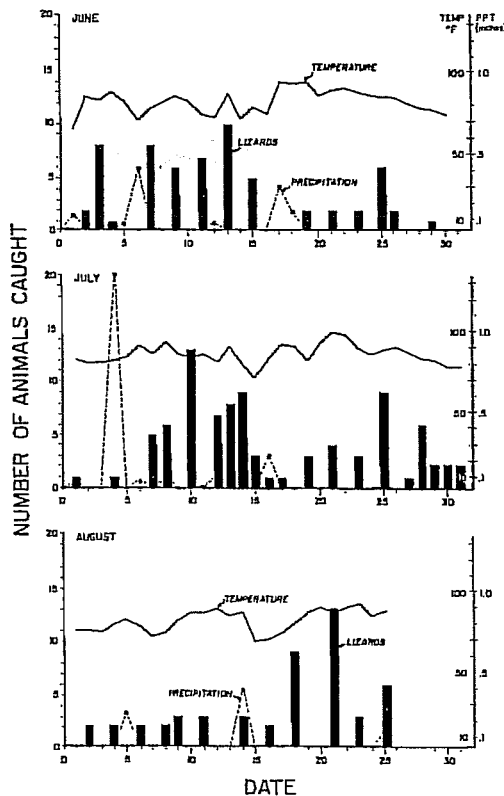


Fig. 16. Relation between catch of *Cnemidophorus* at Blue River and precipitation and temperature.

caught after spring and fall rains may not necessarily indicate large populations in the habitat where they are caught. They often travel a mile or more from summer foraging grounds to winter hibernacula, and many unsuitable foraging areas are often traversed enroute. Better estimates of the number of snakes, lizards, or frogs in a particular habitat can be obtained in June and July, after the spring migrations and before the appearance of young.

Length of Trapping Period

Because of seasonal activity, staggered reproductive strategies, and migration patterns, it is

impossible to adequately sample all species present in an area at the same time. Thus, the length of time necessary to obtain a good estimate of the diversity of animals present is an important factor in evaluating any census method.

Density and diversity of frogs, snakes, and turtles at Portage and turtles at Blue River were high and the trapping periods long; thus the trapping time needed to show species composition and abundance at different seasons could be determined by examining the catch over the entire period. At Portage, drift fences were in operation for 162 days, but only 3-5 continuous days of trapping during optimum weather conditions were needed to capture the most common species of reptiles and amphibians.

The three most common species of turtles were taken in 3 days during the laying season in June at Portage. The fourth species, *Trionyx spiniferus*, was not caught in the nesting season but was taken during the August posthatching dispersal. In 2 days at Blue River, two of the four species of turtles known to nest in this area were caught. The other two never appeared, but they are less common.

In mid-summer, 1 to 3 months of continuous trapping were required at each trapline at Portage to take the four common species of snakes, whereas the same four species were caught in 1 to 4 days in September and October. Summer trapping of the three common species of frogs at the Portage sites required over 1 month, whereas all three were often caught on a single day or at least within 3 days in September and October.

Racerunner population estimates were made with the Jolly stochastic model (Jolly 1965). Catches for 4-day intervals from 30 May to 28 July ranged from 0 to 75, whereas those from three 15-day intervals ranged from 29 to 60 during that time. Omitting the two periods of no catches yields a 4-day interval range of 22 to 75, which is roughly comparable with the estimate given by 15-day intervals.

The catch of all species over the months of trapping in this study showed many periods of low or no success. Since movement normally is associated with favorable weather and migration activity, several short sampling periods staggered throughout the season should give a

better estimate of species composition and populations than a longer period at any one time.

Overall Effectiveness

Overall effectiveness of the fence-trap systems was measured through comparison of catches in areas of known species composition and in areas which were being sampled by other methods. The species composition at the Portage sites has been known from 5 years of searching. All these species at Portage were also taken through drift fence trapping. Also, two species (the glass lizard and tiger salamander) that were recorded in previous years only near Portage were also trapped by drift fences.

At Point Beach, in 5 days of trapping without rain, 3 of the 10 known species of amphibians in the forest were caught. In 5 days, during which a rain occurred, 6 of the 10 were caught. Of the two species not caught by traps, one is normally uncommon and the other was uncommon because of the drought.

The drought conditions apparently affected the sampling at Spring Green. In 2 months of trapping, only 2 of the 12 known species of reptiles in this area were caught. In 15 h of intensive searching in the area during the summer, however, only three species were found.

Two of our study areas were being studied by other researchers. At Long Lake, B. Hellmich (personal communication) marked 420 leopard frogs from 1 April to 10 September. Nearly all of these were caught in an alfalfa field rather than in a marsh, and he estimated the population to be 4,004 individuals. Although about 75 leopard frogs were seen in the alfalfa field at the time the fence-trap systems were set up in the adjacent marsh, only four were caught in two 6-day trapping periods. This illustrates the need of setting several fences throughout an area in various habitats. Hellmich also saw about 20 toads, 30 green frogs, and 70 wood frogs (mostly in the marsh) in the area. While trapping in each of the two 6-day intervals, we caught 3 of the 4 anuran species known from the area. Thus the use of drift fencing to determine species composition appears to be effective.

Before the trapping system was set at Point Beach, all the *Rana sylvatica* were censused in two 9×27 -m areas by walking back and forth and counting frogs. In 2 h and 46 min, 120 *R.*

sylvatica, mostly juveniles, were found in area A and two in area B. Drift fence line A (30 m) produced 75 *R. sylvatica* and line B (15 m) produced 20. The difference between the catches and the frog counting represents time-of-day bias. Counting was done from 1512-1758 CDT, whereas the traps were open for 24 h. When a trained person walked back and forth across the quadrat, more frogs were seen, but some of them could have been counted more than once. The drift fence was stationary and caught only the frogs moving to it. Collecting proceeded 24 h/day with little effort after the initial set-up, and with little observer bias. Therefore, many areas can be compared by different people during the same time span and relatively comparable data can be obtained.

Population estimates (Jolly 1965) of the number of six-lined racerunners caught at line 2 at Blue River ranged from 0 to 75 ($\bar{x} = 36$) for 11 4-day intervals. This compares with 45 *Cnemidophorus* caught by the fence during the same time period. If the two 4-day periods when population estimates were zero due to severe weather conditions are eliminated, then the mean population estimate corresponds closely to the actual number caught over the summer (45 compared to $\bar{x} = 44$ estimated).

The transect of 10 funnel traps set perpendicular to Blue River fence No. 2 caught marked animals a maximum of 20 m from the fence. Since the next traps were 40 m on each side of the fence, these results suggest that a drift fence collects from an area less than 80 m wide for relatively sedentary species such as *Cnemidophorus*. Funnel traps without drift fences were effective for capturing *Cnemidophorus*: 36 captures in 10 traps over a 41-day period compared with 45 in 60 m of fence with 12 traps. Funnel traps without fences seem to be an effective way of sampling some lizard populations. Further trapping is needed to compare population estimates.

Manpower and Cost

The most time-consuming part of running drift fences is set-up time. It took two people $1\frac{1}{2}$ h each to establish 30 m of aluminum fence with 8 pit traps and 2 funnel traps. A dozen animals were removed and marked from 15 m of fence in 5-10 min. Even when large numbers of

animals were caught, removal time was relatively short. For example, 267 animals were removed from 41 m of fence and marked by two people in less than 1 h. Distance between trap-lines dictated the number which could be checked per day. A site with a total of 90 m of fence would require $\frac{1}{2}$ day to set up, and could be checked in less than 1 h by one person; moreover, if the sites were less than an hour apart, four sites could easily be done per day.

Once the fence was established, it was convenient to leave it open only during ideal weather conditions, particularly when several sites 25-50 km apart are being monitored. Funnel traps were picked up and pit traps covered when not in use. A 15-m fence with pit and funnel traps was removed by one person in 5 min. The initial cost was about \$50 for 30 m of fence with traps. However, the fence can be used for many areas. Operating cost for eight sites would be about \$1,200 for an entire season.

Recommended Procedures

Materials

Although somewhat more costly and heavier to carry than screening, aluminum valley seems to be the best fence material. It should be more economical over longer periods since it is far more durable than screen. Hardware cloth was not used because of the same disadvantages of the screen and it costs as much as aluminum valley. C. R. Shoop (personal communication) has been using a plastic-coated screen successfully for salamanders in Massachusetts. It is lighter than aluminum and less expensive, but its durability needs testing.

The following materials are recommended for fencing and traps: aluminum valley (or flashing), 1-m angle iron stakes (two per fence line), 18.9-L plastic ice cream buckets with lids, 7.6-L cans with funnel rims (Fig. 1) and lids, and two-door funnel traps (Fig. 2).

Time of Trapping

Season

In Wisconsin, from 1 April through 15 June, all of the species of reptiles and amphibians using a terrestrial habitat may be expected to be

active. Trapping in the early part of April is necessary to collect many terrestrial and fossorial salamanders (*Ambystoma maculatum*, *A. laterale*, *A. tremblayi*, and *A. tigrinum*). A trapping period in early September will also produce these species when the young are leaving the ponds. However, in dry years, reproduction may not be successful, and a fall trapping period would not be necessary.

Trapping in late April-early May yields fewer species of salamanders, but most species of frogs and many snakes are moving. In late May, most species of snakes and lizards may be caught, but fewer species of frogs and salamanders. During the first 2 weeks of June, turtles begin to nest.

For a complete assessment of the herpetological community, at least four trapping periods of 3 to 5 days each coinciding with rain in early April, late April-early May, and late May and mid-June are recommended. The following exceptions apply if the area to be censused is farther than 3 km from water: (1) the June trapping period is not necessary because turtles seldom go that far in search of a nesting site; and (2) the early April trapping and late April-early May periods are not needed because salamanders and frogs seldom move more than 3 km between breeding sites and summer home ranges.

Weather

Drift fences may be put in at any time, but traps should be kept closed until rain is expected. The most productive trapping period for amphibians is in the 24 h after a rain starts. They will be active on the surface while temperatures are greater than 4° C.

In Wisconsin, snakes and lizards become active after rains when air temperatures reach 21° C or higher. Overcast humid days above 15° C are ideal for catching aquatic turtles in terrestrial habitats.

Habitat Assessment

This section presents a simplified method for evaluating the habitat characteristics in the sample area and the types of reptiles and amphibians that might be present. This evaluation is necessary for proper trap selection and placement. The analysis is specific to the northern midwestern states, but it can be modified for any site.

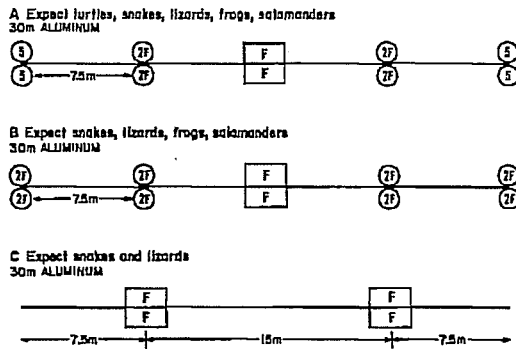


Fig. 17. Type and placement of traps dictated by expectation of catch based on habitat assessment. The symbols S, 2F, and F refer to the positions of 18.9-L pit traps, 7.6-L pit traps with funnels, and funnel traps.

If an area is within 3 km of permanent water, expect all major groups of reptiles and amphibians (Fig. 17A). If the area is farther than 3 km from permanent water but within 3 km of temporary ponds, marshes, or streams, or if the area is heavily wooded, expect snakes, lizards, frogs, and salamanders (Fig. 17B). If a prairie, old field, or savannah is more than 3 km from any open water, either permanent or temporary, expect only snakes and lizards (Fig. 17C).

Position and Length of Fence Line

At least two 30-m lengths of fence with traps should be placed 100 m apart parallel to the vegetation gradient and another 30 m set perpendicular to and halfway between the other two lines (Fig. 18A). If two adjoining habitat types are being assessed, a 30-m fence parallel to the habitat gradient and another 30-m fence perpendicular to the gradient is needed in each area to show the difference between use of an area as a home range and use of an area as a migratory corridor. In situations where the width of the habitat does not allow 30-m lengths of fence to be used, 15-m lengths on either side of the line parallel to the strip can be used (Fig. 18B). Areas which are less than 15 m wide need not have any perpendicular fences.

Installation

It is recommended that V-shaped trenches for

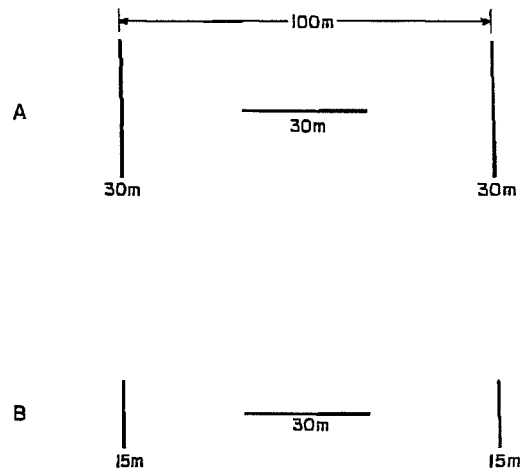


Fig. 18. Proposed placement of drift fences.

the fence lines be about 10 cm deep and about 15 cm wide. A wedge of earth can be removed and then replaced firmly in the trench. One side of the trench should be vertical for a tight fit with the fence. The aluminum can be easily cut and bent to go around logs, rocks, or tree roots (Fig. 3). Mounds of soil and rocks can then be placed over those sections to hold them firmly in place. If more than one roll of aluminum is used, they can be joined together by a strip of duct tape on each side after overlapping the aluminum 6-8 cm.

If weather conditions are right for immediate trapping, 2.5 cm of water should be placed in each pit trap. The water prevents dehydration and also kills ants, beetles, shrews, and mice which might otherwise kill or injure other small animals. Holes drilled 2.5 cm up on the sides of the can allow overflow. Digging the pit slightly deeper in the center leaves a cavity for excess water to drain, preventing rain from filling cans and allowing escapes. A wet piece of cloth should be placed in funnel traps to prevent desiccation of the specimens.

Operation

Traplines should be open continuously for the 3- to 5-day trapping period and checked at least every other day. They should be checked within 24 h after heavy rains because of the likelihood of increased animal movement as well as the accumulation of water in the traps. Animals should be removed, identified, and, if necessary,

measured, tallied, marked, and released 2 or 3 m away on the opposite side of the fence.

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Appendix

Common and scientific names of reptiles and amphibians cited in text or taken during study in southern Wisconsin.

REPTILES

Turtles

Snapping turtle	<i>Chelydra serpentina</i>
Blanding's turtle	<i>Emydoidea blandingi</i>
Ornate box turtle	<i>Terrapene ornata</i>
Painted turtle	<i>Chrysemys picta</i>
Map turtle	<i>Graptemys geographica</i>
Spiny soft-shell turtle	<i>Trionyx spiniferus</i>

Lizards

Glass lizard	<i>Ophisaurus attenuatus</i>
Six-lined racerunner	<i>Cnemidophorus sexlineatus</i>

Snakes

Hognose snake	<i>Heterodon platyrhinos</i>
Smooth green snake	<i>Ophedryx vernalis</i>
Blue racer	<i>Coluber constrictor</i>
Black rat snake	<i>Elaphe obsoleta</i>
Fox snake	<i>E. vulpina</i>
Bull snake	<i>Pituophis melanoleucus</i>
Milk snake	<i>Lampropeltis triangulum</i>
Prairie garter snake	<i>Thamnophis radix</i>
Eastern garter snake	<i>T. sirtalis</i>
Brown snake	<i>Storeria dekayi</i>
Red-bellied snake	<i>S. occipitamaculata</i>

AMPHIBIANS

Caudates

Blue-spotted salamander	<i>Ambystoma laterale</i>
Spotted salamander	<i>A. maculatum</i>
Tiger salamander	<i>A. tigrinum</i>
Central newt	<i>Notophthalmus viridescens</i>
Red-backed salamander	<i>Plethodon cinereus</i>

Anurans

American toad	<i>Bufo americanus</i>
Crickit frog	<i>Acris crepitans</i>
Western chorus frog	<i>Pseudacris triseriata</i>
Northern gray tree frog	<i>Hyla versicolor</i>
Cope's gray tree frog	<i>H. chrysocelis</i>
Spring peeper	<i>H. crucifer</i>
Bull frog	<i>Rana catesbeiana</i>
Green frog	<i>R. clamitans</i>
Leopard frog	<i>R. pipiens</i>
Wood frog	<i>R. sylvatica</i>

**SUMMARY OF HERPETOLOGICAL
COMMUNITY STUDIES**

A Chronological Bibliography, the History and Status of Studies of Herpetological Communities, and Suggestions for Future Research

by

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Abstract

The Chronological Bibliography of Herpetological Community Studies is used to prepare an historic resumé of the field. The taxonomic and geographic distributions of the studies are described, and the contributions of studies of special themes and habitats are identified. Community studies are derived from classical natural history investigations with input from many other disciplines. The clearest recent trend is the sophisticated mathematical analysis of community structure exemplified by the works of Pianka, Inger, and Schoener. Energy flow studies have begun to appear, and the inevitable controversies have sprung up. Another recent development is the large amount of pertinent research being sponsored by a multitude of governmental agencies. The symposium contributions summarized reflect the current state of the art of herpetological community studies. Suggestions for the future include the need for a rigorous examination of our operating assumptions, such as the role of competition, the amount and availability of the resource bases, and the ecological reality of arbitrary communities. The role of sociality needs to be examined in a community context. New field and analytical techniques need to be developed, and long-term studies should receive high priority. Herpetologists working on government projects should take the responsibility for publishing their findings in scientific journals. Detailed prior planning is seen as the most important factor in determining the success of a herpetological community study.

Though research on herpetological communities has expanded greatly in recent years, it still claims only a small proportion of the herpetological literature. For instance, 246 herpetological titles were published in the 1978 volumes of *Copeia*, *Ecology*, *Herpetologica*, and the *Journal of Herpetology*. Of these, only eight (3%) were sufficiently community oriented to include

in the Chronological Bibliography of Herpetological Community Studies following this paper. Since all noncaptive reptiles and amphibians live in communities where they interact with other organisms, the opportunities for community research are virtually limitless. This paper is intended to analyze past community studies, to determine their strengths and weaknesses, and to make suggestions for the future that will encourage further research into an area rich in investigative opportunities.

¹Deceased: Died at Gainesville, Florida, on 10 December 1981.

In order to see where we are going, it is instructive to see where we have been. Accordingly, the first part of this paper reviews the historical development of herpetological community studies and defines the major driving forces and trends within the field. The raw data for this review are the contents of the bibliography. After the historical summary, the current status of herpetological community studies is defined based on a resumé of the papers in this volume and the current literature. Finally, the perceived trends in these studies are defined, and recommendations are made in which progress can be made in the most productive directions.

The Chronological Bibliography of Herpetological Community Studies was compiled by following the community criteria laid down in the Preface; that is, the studies that are listed involve three or more reptile or amphibian species living in the same area. There should also be enough ecological or behavioral information to enable species comparisons, and their interactions (or lack thereof) may be deduced. The rather extensive literature on mimicry was omitted, largely because most of the material is still very theoretical and speculative, and field tests are lacking. We have not seen all of the studies listed in the bibliography, and several citations were included on the basis of information provided by other authors. We have tried to make the bibliography as complete as possible, but new references are continually coming to our attention. Foreign studies are particularly likely to have been overlooked. It is complete enough, however, to provide an accurate basis for the historical resumé.

History of Studies of Herpetological Communities

Historical Resumé

The origins of studies of herpetological communities are not very remote, although their roots are deeply buried in the explorations of the early collectors and naturalists. Nothing published in the 19th century was community oriented, and interest in the ecological relationships of sympatric reptiles and amphibians grew slowly in the early 1900's. The development of the study of herpetological communities paral-

els that of the study of ecology itself, with perhaps a 10- to 15-year lag in most subject areas.

As befitting an infant discipline, early studies were descriptive. Picado's (1913) description of Costa Rican bromeliad faunas included reptiles and amphibians, and his holistic approach could well be emulated by present and future workers. Wright's *Life Histories of the Anura of Ithaca* (1914) was an early example of what could be done by an astute observer collecting data at one site over a period of years, and this type of detailed description of the long-term average phenology of the frog fauna has been rarely duplicated for other areas. During the 1920's, similar studies appeared; interestingly enough, all dealt with snakes: Klauber (1924) in southern California, Brimley (1925) in North Carolina, and Loveridge (1927) in Massachusetts. These studies were mainly concerned with documenting activity and, to some extent, habitat preferences.

The same themes were present in the 1930's. Conant (1938) wrote of reptilian activity patterns in Ohio, and Klauber (1939) contributed a study on snakes. Habitat preferences began to be emphasized: Mosauer (1935) described the fauna and its adaptations in a sand dune area, Humphrey (1936) documented altitudinal distributions of Arizona rattlesnakes, and Dunn (1937) produced a paper amplifying Picado's (1913) original observations on bromeliad herpetofaunas. During this same decade, the work of Uhler et al. (1939) on snake food habits foreshadowed the proliferation of similar studies so important in modern community analyses.

The 1940's saw the emergence of the modern type of descriptive study that integrates most of the important aspects of the biology of the organisms—their demography, abundance, habitat preferences, food habits, activity patterns, and enemies. Fitch (1949), who continues to be one of the most active researchers in the field (this volume), produced an excellent integrated study on California snakes, and Hairston's (1949) report on the ecology of Appalachian salamanders is another fine example. An important development during this period was the initial attempts to quantify animal abundances and other important ecological variables. Quantitative descriptions of populations, their food habits, and their habitat preferences are the raw materials for modern community analyses.

The next decade and a half (1950-65) was

Table 1. *Number of papers dealing with each taxonomic and geographic segment of the herpetofaunal community. Some papers fit into more than one category and may be tabulated several times.*

Region and taxon	Africa	Asia ^a	Australia	Central America ^b	South America	Europe	Totals
Tropics							
Reptiles and amphibians	10	8	1	16	6	—	41
Lizards	7	2	1	35 ^c	1	—	46
Snakes	6	2	8	2	2	—	20
Turtles	—	—	—	—	3	—	3
Crocodilians	—	—	—	—	4	—	4
Frogs	6	6	—	8	5	—	25
Salamanders	—	—	—	1	—	—	1
Totals	29	18	10	62	21	—	—
Temperate Zone							
Reptiles and amphibians	—	—	2	19	2	1	24
Lizards	12	—	9	40	5	1	67
Snakes	4	—	2	43	—	—	49
Turtles	—	—	—	2	—	—	2
Frogs	3	1	2	20	1	—	27
Salamanders	—	—	—	13	—	—	13
Totals	19	1	15	137	8	2	—

^aIncludes the East Indies.

^bIncludes the West Indies.

^cIncludes 27 studies restricted to the genus *Anolis*.

largely a period of consolidation and amplification of the trends already established. Habitat preferences continued to be a favorite topic; guts (mostly snake) were analyzed, and other biological characteristics of sympatric species were examined. Increasingly more emphasis was placed on species interactions, and competitive exclusion became a key phrase and focus of analysis (Hairston 1951; Fouquette 1954; Milstead 1957a, 1957b, 1957c, 1965; Pianka 1965). As in other areas of ecology at the time, competition was assumed to be an organizing force in reptile and amphibian communities; however, no one tested the assumption.

In the mid-1960's, community studies had matured to the point where comparisons between communities were being made. The early studies of Brown and Alcalá (1961) in the Philippines, Heatwole and Sexton (1966) in Panamá, and Pianka (1965) in the North American deserts are the first models of a field that has burgeoned in the last 10 years. Pianka has con-

tinued to be highly productive both in theoretical community comparisons and in natural history studies. At the same time, Barbault (1967) began detailed community studies that would ultimately provide the greatest wealth of quantitative information on entire herpetological communities available today.

Taxonomic and Geographic Distribution of Studies

A tabulation of the taxonomic distribution of the studies in the bibliography (Table 1) reveals that there have been only a few on crocodilians and turtles. The former group is never very speciose in any one area, and crocodilian "communities" are scarce; however, it is surprising that turtles have not received more attention. They are abundant and easily caught in many places, and multispecies aggregations are common. Lizards are often common, diurnal, and

conspicuous, and they have been the subject of the majority of studies in both temperate and tropical habitats. Twenty-seven of the total of 33 tropical lizard studies have been carried out on the genus *Anolis* in the West Indies.

Our list of the geographic distribution of the studies in the bibliography is probably biased toward studies in Australia, Africa, and the New World; even so, relatively few community studies have been done in Asia and Europe. The great majority of temperate zone work has been done in North America, and a large proportion of the tropical studies have been done in Central America, including the West Indies. The efforts of a few very prolific workers are largely responsible for several of the totals: Barbault in tropical Africa, Inger in tropical Asia, Schoener in West Antillean *Anolis*, and Pianka in temperate Africa and in Australia.

Special Study Themes

Several ecological and taxonomic systems have received a disproportionate share of attention. The system represented by the genus *Anolis* in the West Indies mentioned above is one of the best examples. Under the guidance of Ernest Williams at Harvard University, many outstanding theoreticians, systematists, ecologists, and behaviorists have developed an impressive body of data and theory that will provide material for integrative studies of evolution and ecology for many years to come.

Other taxonomically-based systems that have been exploited are the North American natricine snakes (Fitch 1941; Hebrard 1951; Carpenter 1952; Fouquette 1954; Fleharty 1967; Burgardt 1968; Hebrard and Mushinsky 1976, 1978; Mushinsky and Hebrard 1977a, 1977b; Kofron 1978), whiptail lizards (*Cnemidophorus* and *Ameiva*; Milstead 1957a, 1957b, 1957c, 1965, 1972, 1977; Medica 1967; Asplund 1968b; Hillman 1969; Schall 1973, 1977; Scudday and Dixon 1973; Scudday 1977; Mitchell 1979; Cuellar 1979), sea snakes (Shuntov 1971; Voris 1974; Dunson 1975; Heatwole 1975a, 1975b; Limpus 1975; McCosker 1975; Minton and Heatwole 1975; Dunson and Minton 1978; Redfield et al. 1978) and rattlesnakes (Humphrey 1936; Darnman 1961; Pough 1966; Klauber 1972). All of these groups, except the rattlesnakes, are largely diurnal forms that are often abundant and have enough species in a genus so that several similar

forms may occur in a given spot.

Other faunas that have contributed the raw materials for a large number of papers are desert reptiles (54 papers) and calling and successional studies of frog ponds (21 papers). Again, the attractive combination seems to be an abundance of animals in a habitat where they are easily observed and collected.

Food habits studies are basic to the understanding of any animal community. The bibliography includes 19 titles which are primarily descriptions of the food habits of coexisting species. Almost half of these are studies of snakes, whereas most of the other studies are divided between lizards and amphibians.

Special Habitats

Several specific kinds of habitat have been singled out for special study. The common thread drawing these studies together is that they deal with habitats that either concentrate animals or that have naturally high populations. For instance, bromeliads concentrate both amphibians and reptiles, especially in the dry season (Picado 1913; Dunn 1937; Smith 1941; Neill 1951), and their faunas are rather easily characterized. Similarly, Funderburg and Lee (1968) and Lee (1968, 1969) investigated the herpetological associates of Floridian pocket gophers (*Geomys*), other mammals, and cabbage palms.

Islands have been a favorite laboratory for evolutionary studies since Darwin and Wallace, and they are beginning to be recognized as good places to study community interactions. An attractive feature of most archipelagos is that similar biotic communities tend to be repeated under a similar climate, but the biogeographic history of each island produces a distinct combination of species. Thus, each island can be viewed as a separate evolutionary "experiment." The *Anolis* students mentioned above have exploited the insular features of their fauna to such a degree that there are few comparable mainland studies. Other workers who have successfully used island systems are Soulé (1966), Case (1975, 1978); Dunham et al. (1978); Case et al. (1979); and Bennett and Gorman (1979).

In the early 1950's, a noteworthy subset of herpetological communities spawned a diverse literature. Anchored by Woodbury and his students in Utah, studies of hibernating aggregations of reptiles (most often snakes) became

popular. The Utah dens have produced several of the few long-term community studies, and the availability of large numbers of research animals has provided opportunities for detailed insight into the biology of the snakes involved. The paper by Brown and Parker in this volume is the latest in these studies, and its conclusions hold little promise for the future of this important study system that has produced so many articles (Woodbury and Hansen 1950; Woodbury 1951; Woodbury and Parker 1956; Hirth 1966; Hirth and King 1968; King 1968; Hirth et al. 1969; Parker and Brown 1973). Other workers that have studied hibernating aggregations of reptiles and amphibians are Neill (1948), Carpenter (1953), Storm (1955), Cooper (1956), and Drda (1968).

Natural History Studies

Modern community studies, even highly theoretical works, have evolved from origins in classical descriptive natural history. Whereas early workers were content to describe communities, many recent studies probe the questions of "how" communities function and "why" communities are structured as they are. Quantitative instead of just qualitative approaches are becoming more common, and new field and analytical techniques are constantly being developed.

Probably the best known herpetological community is that of the University of Kansas Natural History Reservation. For more than 30 years, Henry Fitch and his students have studied the herpetofauna of this tract of land. Much of the information was published as a series of autecological monographs, but recently the data are being analyzed for community patterns (Henderson 1974; Fitch, this volume). There still remains a wealth of information for further integration.

Natural history studies make up the bulk of the bibliography, and the list of recent contributors is long. Outstanding individual records include Rand (1961, 1962, 1964, 1967; Rand and Humphrey 1968; Myers and Rand 1969; Rand and Williams 1969); Heyer (1967, 1973, 1974, 1976a, 1976b; Dixon and Heyer 1968; Heyer and Bellin 1973); Heatwole and Sexton (Sexton et al. 1964; Heatwole 1966, 1975a, 1975b, 1976; Heatwole and Sexton 1966; Test et al. 1966;

Sexton and Heatwole 1968; Minton and Heatwole 1975); Duellman (1960, 1965, 1967, 1978); Dixon (Dixon and Medica 1966; Dixon and Heyer 1968; Scudday and Dixon 1973; Dixon and Soini 1975, 1977; Staton and Dixon 1977; Henderson et al. 1978, 1979); Milstead (Milstead et al. 1950; Milstead 1953, 1957b, 1960, 1965, 1972; Milstead and Tinkle 1969); and Hebrard and Mushinsky (Hebrard and Mushinsky 1976, 1978; Mushinsky and Hebrard 1977a, 1977b).

The most productive group in the quantitative exploration of herpetological communities has been Robert Barbault and his collaborators, Claude Grenot and Roland Vernet, of the Laboratoire de Zoologie of the Ecole Normale Supérieure in Paris. Publishing since 1967, Barbault has authored or coauthored more titles (19) in the bibliography than any other author. Starting in Africa, he quantified the populations, biomass, habitat use, activity cycles, and trophic structure of the reptile and amphibian communities of the Ivory Coast savannahs (Barbault 1967, 1970, 1971, 1972, 1973, 1974a, 1974b, 1974c, 1974d, 1975a, 1975b, 1976a, 1976b, 1976c, 1976d). Transferring his experience to México, he continued the same types of studies in Chihuahua (Barbault 1977; Barbault and Grenot 1977; Grenot et al. 1978; Barbault et al. 1978). Grenot and Vernet also investigated North African herpetofaunas (Grenot and Vernet 1972a, 1972b; Vernet and Grenot 1972a, 1972b). In recent publications, Barbault and Grenot processed their data using niche overlap theory, and their analyses tend to converge on those of Pianka (Grenot et al. 1978; Barbault et al. 1978). This wealth of material is little known in North America and has not been incorporated into recent reviews (Pianka 1977; Schoener 1977).

Three recent authors have made outstanding contributions by cataloging and analyzing some of the most complex herpetological communities known. Dixon and Soini (1975, 1977) and Duellman (1978) worked intensively for many years on the Amazonian slopes of Peru and Ecuador. Both sets of studies stem from similar sorts of backgrounds: strong systematic training and experience, blended with a natural history approach to the interpretation of communities. These works should provide copious raw material for developing hypotheses on the structure and function of tropical communities.

Other Disciplines

Many other herpetological disciplines such as systematics, physiology, and autecology have contributed to the development of community studies. The debt to alpha taxonomy is obvious but often overlooked. Many ecologists are unaware of the taxonomic problems in their study area and often do not wish to become involved in their solution. At a minimum, every ecological study should deposit properly prepared voucher specimens in a public museum. Neglect of the nuts and bolts of classical taxonomic herpetology can lead to confusion and imprecision in community studies.

Often a wide gulf exists between laboratory physiologists and field ecologists. The few people that have made an attempt to bridge the gap have provided valuable insight into community function that could not be gained in any other way. Clark (1967), Sexton and Heatwole (1968), and Pough et al. (1977) investigated habitat selection and water loss in snake, lizard, and frog communities; Ruibal (1961) and Schall (1977) looked at thermal adaptations in lizards; and Burghardt (1968) studied innate food habits in a water snake community. Fleharty (1967), in the most complete laboratory analysis of a community to date, studied food habits, water loss, specific gravity, and oxygen consumption in garter snakes. The common feature of these studies is that laboratory and field studies were integrated to provide a unique understanding of the communities involved.

Autecological studies have been, and will continue to be, the basis for most of what we know about the ecology of reptiles and amphibians, and there is much in these studies that can be used in community syntheses. However, it is important to remember that a community has properties greater than the sum of the parts, and single species orientations can be misleading in a holistic analysis.

Recent Studies

The greatest number of papers in the "Modern Period," dating from the mid to late 1960's, still deals with "natural history" subjects such as population size and fluctuation, behavior, and food and habitat preferences. These are becoming more and more useful in gauging commu-

nity interactions for several reasons: past experience has indicated which ecological variables are most likely to yield useful information, comparative studies are much more common, and techniques of studying communities have become more sophisticated. In spite of these developments, the most distinctive trend in recent herpetological literature is the application of theoretical, mathematical approaches to community analysis. These studies will be examined in detail below. Other recent developments in the literature are the studies of energy flows through reptile and amphibian populations, three recent controversies that remain undecided, and the accumulation of a vast body of knowledge buried in government reports.

Theoretical Studies

As studies of herpetological communities became more quantitative in the 1960's, theoretical analyses became possible. Species and the communities they formed were viewed as active agents in dynamic evolutionary systems. Words like "competition" and the "niche" became common, and differential equations proliferated. The concept of strategies, such as reproductive or feeding strategy, was developed, and resource partitioning analyses were extended beyond mere food habits studies. Space, structural features of the habitat, and the time of day or year were also seen as vital resources.

The earliest papers with significant theoretical analyses include Hairston (1951) on Appalachian salamanders, Fouquette (1954) using garter snake food habits, Milstead's series (1957a, 1957b, 1957c) on Trans-Pecos whiptails, and Colette (1961) analyzing the correlation between *Anolis* ecology and morphology. Since then, theoretical considerations have been a large part of many papers, and the development of techniques of analysis have been a major effort for many authors. Three of these workers stand out, both because of their prolific output and the ingenuity, depth, and novelty of their community analyses.

Eric Pianka (1965, 1966), borrowing techniques from the avian community studies of Robert MacArthur, was a leader in applying quantitative techniques to the testing of hypotheses of community structure. He has continued to develop and refine his analyses, and his comparative approach, using widely dispersed

diurnal desert lizard systems, has contributed to the robust nature of his conclusions (Pianka 1969a, 1971, 1973, 1975; Pianka et al. 1979). Pianka's emphases have been on the detection of the effects of interspecific interactions, primarily competition, on structure within communities, and the elucidation of geographic patterns of lizard diversity. His approach has been fruitful and, as a result, more is known about ecological characteristics of diurnal desert lizard communities than for any other group of reptiles or amphibians (Pianka 1975, 1977). Although concerns for the structural dynamics of entire lizard communities has dominated his work, Pianka has not neglected the natural history of small segments of communities or even single species (Pianka 1969b; Pianka and Pianka 1976; Huey and Pianka 1977; Pianka and Huey 1978; and several other papers outside of the scope of this bibliography). Without this solid natural history base, Pianka's more esoteric theoretical conclusions would be much less acceptable to the general herpetological scientific community.

During the same period, Tom Schoener was adapting a system for measuring structural habitat developed by Rand (1964) to quantify niche characteristics in communities of West Indian *Anolis*. Schoener's earliest studies dealt with single species interactions, but he soon used the same techniques to describe patterns and consequences of resource use by multispecies communities. Patterns analyzed have included animal size relations (Schoener 1969, 1970b) and food and habitat use (Schoener 1968, 1970a, 1974a, 1974b, 1975; Schoener and Gorman 1968; Schoener and Schoener 1971a, 1971b).

Robert Inger and his collaborators have applied innovative analytical techniques to large bodies of community data from the Asian tropics and subtropics (Lloyd et al. 1968; Inger and Colwell 1977; Inger 1980). The questions he deals with (habitat use, species packing) are similar to those studied by Pianka, but the approaches are rather different. Much of the difference derives from problems of scale; Pianka treated 4 to 29 sympatric lizard species in his studies, but Inger treated more than 100 species of reptiles and amphibians. Inger has also contributed to our knowledge of the ways that small segments of faunas interact (Inger and Greenberg 1966a, 1966b; Inger 1969), and Inger and Greenberg (1966a) conducted one of the few field experiments on amphibians.

In addition to the prolific workers cited above, a number of other herpetologists have contributed creative analyses to the further development of our theoretical body of knowledge. They are too numerous to list here, but a few deserve mention for the amount and quality of their work: Crump (1971, 1974, this volume), Wilbur (1972; Wilbur and Collins 1973), Heyer (1973, 1974, 1976b; Heyer and Berven 1973), Hurtubia (1973; Hurtubia and di Castri 1973), Fuentes (1976), Moermond (1974, 1979), Huey (Huey and Webster 1976; Huey and Pianka 1977; Pianka and Huey 1978; Huey 1979; Pianka et al. 1979), and Case (1975, 1978; Case et al. 1979).

Energy Flow Studies

Strangely enough, herpetological communities have largely escaped the analyses based on energy flows to which other vertebrates were subjected during the era of the International Biological Program when funding for system-oriented ecological research was most easily obtained. Perhaps the thought was that, even at high densities, reptile and amphibian metabolism was so low compared with mammals and birds that their role in community energetics was negligible. Two recent studies indicate that this generality is probably untenable. Burton and Likens (1975a, 1975b) showed that salamanders in a New Hampshire forest constitute as much of the animal biomass as any other group of vertebrates, and that energy flow through the salamanders is about 20% of that through the birds in the same ecosystem. Bennett and Gorman (1979), working on the arid West Indian island of Bonaire, concluded that lizards were major consumers, and their daily energy requirements exceeded those of small mammal faunas in temperate zone systems. Clearly the assumption that reptiles and amphibians can safely be ignored in analyses of ecosystem energetics needs reexamination, especially in tropical systems.

Controversy

Any field of human endeavor ultimately generates controversy, but the study of herpetological communities seems to be, with few exceptions, relatively free from disagreement. This

situation is partly good in that it has allowed a free and objective interchange of ideas without the barriers that are artificially erected when differences of opinion become polarized. On the other hand, we believe that the theoretical underpinnings of much of our work has not been adequately examined, and many operating assumptions are accepted without sufficient review. We will return to this idea in the section on suggestions for the future. There are three theoretical areas with opposing views in the papers of the bibliography. One has very little associated data, and the other two have data that are interpreted in two different ways.

The first is the explanation by Janzen (1976) for an apparent lack of reptiles in Africa when compared with tropical America. Using sweeping correlations, Janzen concluded that the community of scavengers supported by the grazing herbivores in Africa also suppressed the reptile populations. Kreulen (1979) took issue and responded with other correlative observations. Janzen's (1979) reply contained no new information but suggested some tests for his hypothesis.

The second controversy has developed over explanations of the sizes of individuals of the lizard genus *Uta* on islands in the Sea of Cortez. Soulé (1966) concluded that the size of utas on islands was determined by the competitive pressure from other iguanid species present. With the collection of more data and further analysis, Dunham et al. (1978) found other variables, such as number of perennial plant species, to be equally well correlated and suggested caution in evaluating correlative data with the *a priori* assumption that competition is the community organizer. The latter authors suggested several ways to remedy the problems that they see in many similar studies.

The third area of controversy lies in differing interpretations of the effects of competition in larval amphibian communities (Heatwole, this volume). Wilbur (1972) and Wilbur and Collins (1973), on the basis of extensive experimentation with *Rana* and *Ambystoma* larvae, concluded that competition was one of the major organizers of many tadpole communities. Heyer (1976b) disagreed, and based on his own studies from Thailand, Panamá, and the eastern United States, concluded that predation and random factors were usually responsible for observed tadpole community structure, and that interspecific competition was not.

These controversies seem to be rather different, but there is a common thread running through them all: the relative importance of predation and competition as organizers in herpetological communities. Janzen's (1976) hypothesis that predation is a major determinant is based on little data and much speculation, and is obviously intended to be heuristic, but the practical means of testing it are not clear. Soulé's (1966) conclusion that *Uta* size depended on competition was tested, and serious doubt was cast on it. Wilbur (1972) and Wilbur and Collins (1973) pinpointed several areas where they believe competition is operating, but Heyer (1976b) saw only predation pressure or random effects. At least one side in each of these arguments believes that one of the most powerful tools for generating definitive data is community experimentation (Wilbur and Collins 1973; Tinkle and Gibbons 1977; Janzen 1979).

Governmental Reports

Governments at all levels have suddenly become aware of the presence of a large number of animal species that have been ignored in previous planning. Now land and pesticide use, waste disposal, resource development, and a multitude of other governmental activities require a complete vertebrate inventory or environmental impact statement before the project can be carried out. The preparation of these inventories or statements include the gathering of a great amount of potentially useful information on reptile and amphibian communities. Most of the information is buried in reports with limited distribution which are collectively referred to as "gray literature." We have not attempted to examine this literature here, but we believe it should not be ignored in the future. Part of the problem with using it is in determining its reliability, since it is often not reviewed by competent biologists, and voucher specimens are seldom prepared.

Review of the Symposium

The contents of the symposium largely reflect the current status of research into herpetological communities. Heatwole reviews our current knowledge of community structure to set the

stage for the rest of the volume. Crump examines the role of life history strategies as they may affect amphibian communities. Her paper provides several predictions for future research. After the reviews, Wiest describes in detail the anuran succession in a series of Texas ponds, and Jones examines niche relations in West Indian frogs.

Three papers on resource partitioning in snakes follow. The first two are the most recent in a long series of studies on well-known systems. Brown and Parker continue the Utah den series, but recent events appear to indicate that this distinguished series of studies will soon be terminated. Fitch summarizes the food habits of the snakes of the University of Kansas Natural History Reservation. The third paper, by Reynolds and Scott, examines a mammal-eating snake community in Chihuahua, México.

Creusere and Whitford initiate the section on lizard communities. Their paper clearly documents the large amount of individual variation in activity patterns; their work underscores the need to look at individual strategies and not to generalize from observations on total populations. Mautz describes an interesting Mexican cave saurofauna, and Bury provides biomass estimates for a series of Mojave Desert lizard and tortoise faunas.

Scott analyzes an African forest herpetofauna and compares it to previous studies in Asia and Central America.

Three papers describe the attributes of herpetofaunas living on sandy substrates. Werner synthesizes work in the Sinai Desert, Campbell and Christman document faunal succession on sandy sites in Florida, and Smith describes resource partitioning in the most highly adapted sand-swimming segment of the same fauna.

The next three papers describe field techniques for community study that have been proven in extensive studies. Lillywhite used tracking methods to study California snakes, Campbell and Christman used various trapping and collecting methods to gather data on Florida faunas, and Vogt and Hine did the same in Wisconsin.

The mix of papers in the symposium seems to be a fair representation of the current state of herpetofaunal community studies. Many of the subject areas prominent in the historical review are present here: frog pond succession, hypothesis-generating theory, food habits, resource par-

tioning, special habitats, and mathematical analyses.

Suggestions for the Future

The literature review and the symposium contributions point to several clear recommendations for future work. For instance, the general unavailability and unawareness of Barbauld's work in North America underscores the need for much more effective reprint exchange and translation services than we have at present. Recent tendencies to cut back or eliminate foreign language requirements in graduate curricula have certainly contributed to the problem. More personal contacts between workers in different countries would also help.

Another specific area that needs work is the extension of the studies of insular populations of *Anolis* to mainland sites. The West Indian anoles are known in great and voluminous detail, and generalities derived from their study are being extrapolated to many other systems and have threatened to become dogma. However, since these island populations are unusual in many respects, we should be wary of extending the ecological and evolutionary conclusions to mainland forms. From what little that is known, mainland *Anolis* are probably not subject to the same degrees of competitive and predatory pressures as the island ones.

One of the basic assumptions underlying the great majority of resource partitioning studies is that competitive exclusion between species is responsible for the community patterns. Unfortunately, very few attempts have been made to show that competition really exists, and fewer yet have good evidence for its presence. There is a good possibility that competition is an important interaction between island anoles but not between mainland species. Competition is easy to assume and makes a convenient focus for partitioning studies, but we should realize that the best correlations in the world do not prove the importance of competition as a force that structures communities.

One of the few ways to get a better idea of the real importance of competition are experimental studies done in the field. Only two community-level experimental studies have been published so far (Inger and Greenberg 1966a; Cuellar 1979), and more work along these lines will be

needed before we will be able to say whether our assumption has been correct. In the final analysis, interspecific competition will probably prove to be a major determinant of the structure of some communities, whereas it can be ignored in others.

Another neglected aspect of resource partitioning studies is the determination of resource abundance and availability. Theoretically, for exploitative competition to occur, two species must be using a common, limited resource base. The demonstration of these conditions in a given study would greatly strengthen the assumption of the importance of competition. Perhaps more interaction with quantitatively-oriented entomologists and other biologists will help alleviate the problems of sampling food resources.

Related to the problem of the assumption of competition is the arbitrary nature of herpetological communities. Most workers have not attempted to define their version of the community in ecologically meaningful terms. They have dealt with a convenient subset of the animals present, assuming that the interactions between these species are important in determining structure. Pianka (1973, 1977) is one of the few workers in the area to recognize the potential problems. Detailed study of the relations between herpetological species with no concern for other faunal components of the community could be very misleading. For instance, large spiders, scorpions, and centipedes could conceivably be the most important competitors with forest litter reptiles and amphibians, and an analysis of resource partitioning would be grossly inaccurate without including them. Perhaps a clearer picture would emerge if herpetologists thought in terms of "the reptile and amphibian components of the community" instead of the current usage. Pianka (1973) and Heatwole (this volume) would use the word assemblage in the same context.

Another technique that has been underexploited by researchers is the combined field and laboratory study. The few mentioned above have shed a great deal of light on the adaptations of reptiles and amphibians to their environment, and when a comparative approach is followed, many of the proximate causes for observed community patterns become clear.

Comparing the structure of different communities is a useful technique for detecting global patterns. Pianka has been the leader in

developing this method, but the contrasts need not be intercontinental to be useful. Comparisons between a variety of local communities, such as Campbell and Christman's Florida sandhill paper in this volume, can serve to focus attention on faunal patterns that would otherwise be missed. In order to make comparisons between two sites, the data need to be compatible. This is one of the strongest arguments for developing and standardizing techniques that have broad applications in a variety of communities.

The importance of social factors in structuring herpetological communities is almost unknown. Surely the intense territoriality shown by many lizards, frogs, and crocodilians leaves its imprint on the local assemblage. The demographic consequences of high and low population densities have not been investigated. How sensitive are frog choruses, tadpole aggregations, synchronous sea turtle nestings, and other mass activities to low population levels? Most social phenomena in reptiles and amphibians are still poorly known, and their inclusion in an integrated model of community dynamics is a long way in the future.

The development of field techniques for the study of herpetological communities seems to have lagged behind the data gathering in recent years. Papers describing trapping, marking, and census methods were common in the literature of the 1940's and 1950's, but their frequency has dropped in recent years. With field herpetology becoming more and more quantitative, it is necessary to pay more attention to our field methods. Comparisons between techniques are needed, such as Campbell, Christman, Vogt, Hine, and Lillywhite have done in this volume, and methods need to be evaluated over a wide range of habitats. Studies designed for maximum efficiency and utility will then use those methods that give results that can be compared with temperate forest studies because the study techniques have been compatible.

New analytical techniques also need to be developed. Quantitative analyses of community data should be a tool leading to biological understanding and not a goal in itself. If the biological significance of a quantitative procedure is not evident, it should not be used. The checked history of the information theory parameters, H and H' , is a good example. These diversity measurements are useful for quantifying

niche features such as food habits or the use of structural features of the habitat. However, when H' is calculated as a community parameter based on the distribution of individuals among species, its meaning becomes obscure. The community H' has generated much more heat than light, and correlations with some sort of community "stability" or "maturity" seem to be spurious. To say that one community has a higher H' than another carries very little information, and what little there is could be better expressed in more intuitive ways.

Long-term studies are much needed. Almost all of our ideas about herpetological communities derive from short-term "snapshots" of the system. Reptile and amphibian populations vary considerably from year to year; relative species densities fluctuate and some species disappear to be replaced by others. Clearly, conclusions based on one instant in this dynamic system are bound to be misleading. Long-term studies are not easily supported and are often neither cost nor time efficient if volume of publications is the currency of the trade. However, if we are ever going to be able to say with confidence that we understand the functioning of a herpetological community, it will have to be after the community has been studied for many years.

Future studies will inevitably be more concerned with the effects of humans on herpetological communities. There have been a few studies in the past that have dealt with subjects such as urban herpetofaunas, and we foresee a proliferation of these in the future. As humans have an ever greater impact on the environment, we will want to focus on such questions as the community impacts of pesticides and the effects of habitat simplification. Another subject of increasing concern is the evaluation of the results of "island" size on diverse herpetological communities now that it is clear that in the near future there will be no longer any large blocks of continuous natural habitat in many parts of the world.

Herpetologists funded by governmental agencies should shoulder greater responsibilities, taking great pains to see that the data are accurately gathered and that the realities of funding and deadlines are not allowed to compromise the quality of the data and the report. Funding agencies should be made aware of the levels of money and time necessary to do a proper job. If

enough funds are not available, a more limited study should be designed. A major characteristic of many governmental surveys is the attempt to cover vast areas of geography, numbers of taxa, and kinds of habitats by using superficial techniques designed only to satisfy a bureaucratic end. A professional herpetologist trapped into this kind of situation is not likely to derive satisfaction from the results. A second responsibility of those directing governmentally-funded studies is to see that the results are published in a reviewed journal. As mentioned above, the huge volume of gray literature embodied by in-house reports is almost unusable. If the data are worth gathering, they are worth reporting. A third obligation of any biologist, but especially those working on governmental projects, is to deposit adequate series of voucher specimens in an established public museum. This serves to protect both the worker and the government. Government contract officers need to be educated to this necessity and should be prepared to pay their fair share of the costs of specimen preparation and curation. Unfortunately, most agencies are still parasitizing the museums they use, although many curators now have established charges for their services.

Many other recommendations could be made concerning how to increase the effectiveness of community studies, but perhaps the most important one refers to study design. The most sophisticated studies are those that are well planned from the beginning. Pianka, Schoener, and Inger knew what they wanted to measure before they went into the field, and they had a fairly good idea of what questions they were trying to answer. When it came time to analyze the data, they had the necessary measurements. Before a field person devotes a substantial amount of time and other resources to a study, they should as clearly as possible outline the questions they wish to ask and the data they need to answer them. In this way, many descriptive studies could be turned into much more useful examinations of community structure and function.

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