

PIANKA, E. R. 1967. Lizard species diversity. *Ecology* 48:338-351.  
 ———. 1970. Comparative autecology of the lizard *Cnemidophorus tigris* in different parts of its geographic range. *Ecology* 51:703-720.  
 TINKLE, D. W. 1967. The life and demography of the side-blotched lizard, *Uta stansburiana*. Misc. Publ. Univ. Michigan 132.  
 ———, AND R. E. BALLINGER. 1972. *Sceloporus undulatus*: a study of the intraspecific comparative demography of a lizard. *Ecology* 53: 570-584.  
 VINEGAR, M. B. 1972. The function of breeding color in the lizard, *Sceloporus virgatus*. *Copeia* 1972:660-664.

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OBSERVATIONS ON THE ROLE OF THE AMERICAN ALLIGATOR (*ALLIGATOR MISSISSIPPIENSIS*) IN THE SOUTHERN FLORIDA WETLANDS.—It has long been realized that the American alligator is an important component of the Everglades and Big Cypress Swamp ecosystems. The alligator is acknowledged to dig and maintain ponds, called alligator ponds or "gator holes," which provide refugia for aquatic organisms during the southern Florida dry season. This relationship has been widely reported in popular publications (Allen and Neill, 1952; Robertson, 1959; Carr, 1967, 1973; Craighead, 1968) and was recently noted in a textbook (Ehrenfeld, 1970). However no study has actually demonstrated either the use of alligator ponds as refugia or the role of alligators in their maintenance. The purpose of this paper is to present observations and quantitative data, derived from a long-term study of an alligator pond in the Big Cypress Swamp, relating to the ecological role of alligators in the southern Florida wetlands.

The study pond, located in the southeastern Big Cypress Swamp (lat. 25° 44' 50" N.; long. 80° 56' 50" W.), has a mean depth

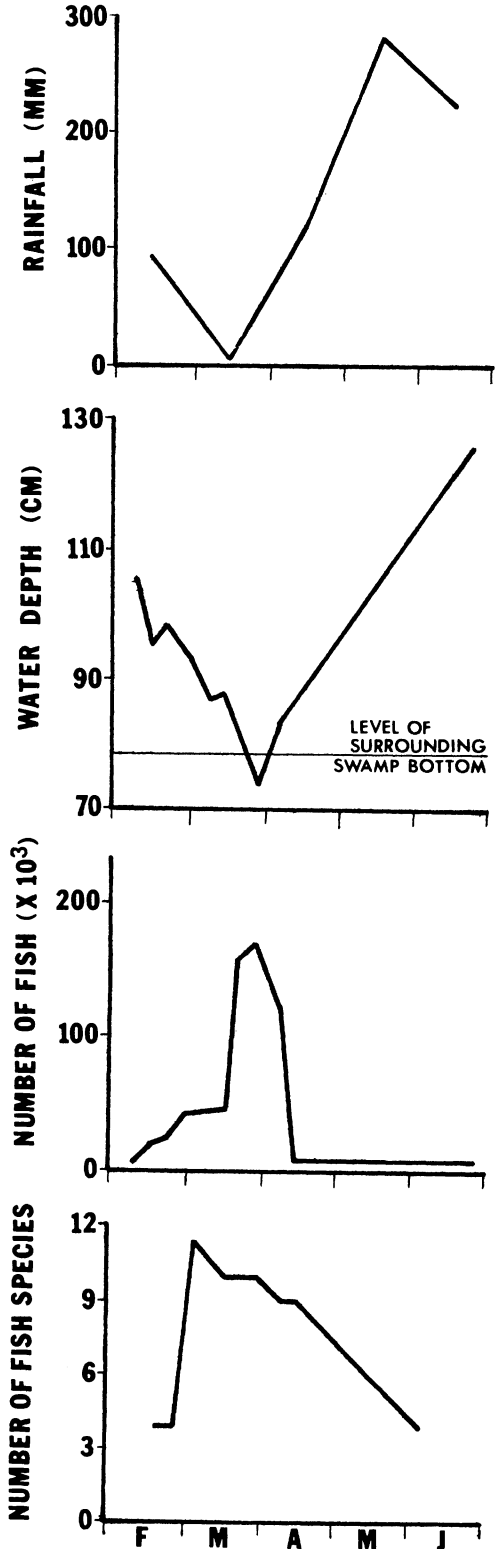


Fig. 1. Changes in rainfall, water depth, number of fish and number of fish species in the pond during the dry season of February to June, 1972.

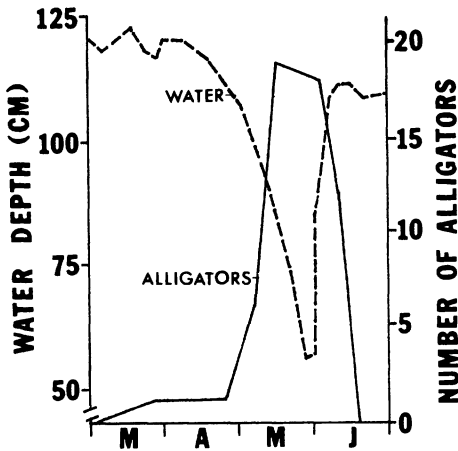


Fig. 2. Water level and numbers of alligators in the pond, March through June 1970.

of 0.8 m and a surface area of 1520 m<sup>2</sup> during high water. A peripheral zone of emergent grass (*Panicum* spp.) surrounds a more open central area which during high water supports submerged *Najas flexilis*. During low water *Najas* dies back to the root system. For most of the year, water in the pond is confluent with surface water of surrounding swamps. In the dry season, water level falls and the swamps dry, isolating the pond.

**Methods.**—I measured changes in number of fish in the pond with two 4-m<sup>2</sup> pull-up traps and four 1-m<sup>2</sup> drop traps. I have discussed elsewhere details of the fish traps (Kushlan, 1974a) and calculations used in estimating fish populations (Kushlan, 1972; 1974b).

**Findings.**—During the dry season as rainfall decreases and water level drops, both the number of fish and number of fish species in the pond increase to a peak at the lowest water level (Fig. 1). The increase is due to movement of fish into the pond from surrounding swamps. The number of alligators in the pond also increases when water level falls (Fig. 2). In the study pond the increase was due to immigration of nonresident juveniles.

Prior to the 1950's the pond supported a large resident population of alligators including several mature individuals and, according to local residents, was the center of an especially productive breeding area. During the 1950's and 1960's, hunting decreased the number in the pond, the last

TABLE 1. EXTENT OF LATERAL ENCROACHMENT OF EMERGENT PLANTS INTO THE POND DURING A PERIOD WHEN FEW (1956–1968) OR NO (1968–1973) RESIDENT ALLIGATORS WERE PRESENT.

Year	Cumulative Encroachment (m)
1956	0
1968	3.0
1970	4.4
1971	4.6
1971	5.7*
1973	7.0

\* Represents encroachment during 1971 when the pond was dry.

large alligator being removed in 1968. Since 1972 the number of two and three-year-old alligators has increased. The lack of large alligators in the pond during recent years provided an opportunity to compare the study pond with more active ones. Ponds in extreme southern Florida with mature resident alligators generally have the following characteristics: 1) both emergent and rooted submerged vegetation are limited to the extreme periphery; 2) there is little sediment in the pond and often the limestone bedrock is visible; 3) usually, although not invariably, a cave or den is dug under a bank, generally under tree roots; 4) a system of trails leads from the pond. In contrast, the study pond lacked den and trails; the sedimentary layer ranged from 0.3 to 2.3 m thick, and, as of 1970, emergent vegetation covered 75% of the pond while submerged plants entirely covered the central area in the late summer and winter.

The movement of emergent and submerged vegetation into the pond has coincided with the reduction in numbers of large alligators. In one location in the pond, grass has encroached 7.0 m in 17 years (Table 1). During the severe drought of 1971, when the pond dried, grass encroached 1.1 m and eliminated 39% of the central area.

Even though alligators are capable of complex digging behavior (McIlhenny, 1935) and excavate dens and deepen ponds during extremely low water level, my observations suggest that it would take no more than the usual movement of a mature alligator to maintain the study pond free of rooted plants. This is because the species of plants which have invaded the pond are intolerant of physical disturbance. For example, a

single passage of a person through the emergent zone was sufficient to uproot the grass in his path. Similarly in 1970 we moved a fish trap into the center of the pond during low water and sampled once. This disturbed the bottom and prevented regeneration of *Najas* at that spot the following summer.

*Discussion.*—The appearance of increasing numbers of fish in the pond during periods when adjacent marshes are drying (Fig. 1) demonstrates that ponds serve as refugia for aquatic organisms. In addition an increased number of species over that found in the pond during high water (Fig. 1) suggests that these are species which are adapted to shallow swamps and which depend on ponds only for survival during drought. Without ponds the persistence of such species in an area characterized by extreme seasonal water level fluctuation is by no means certain. The existence of such refugia is particularly critical in southern Florida where, for biogeographic reasons, a temperate aquatic fauna persists in a subtropical, seasonally fluctuating wetland in which, unlike tropical swamps (Carter and Beadle, 1931), the evolution of elaborate and diverse adaptations for survival through drought has not taken place. It is probable therefore that under natural conditions the alligator maintained species richness within the entire wetland system.

Alligator ponds are merely slightly deeper areas within a vast, shallow expanse of marsh and swampland and, as such, are an unstable sere in a classical hydrarch succession. It is only through the activity of alligators that a disclimatic pond habitat is maintained. Observations at the study pond suggest that the usual movement of large alligators is sufficient to prevent encroachment by successional vegetation. Furthermore the actual digging of caves and excavation of the pond bottom during periods of extreme low water, enlarges the pond's capacity during these critical periods. This is especially important in southern Florida where dry periods are an annual occurrence and prolonged drought a common event because it is during periods of drought that the potential for vegetative encroachment into the pond is greatest (Table 1).

The holding capacity of a pond during low water is a function of its area, depth and plant cover. The activity of alligators serves to increase both area and depth. The

importance of this was demonstrated during the prolonged drought of 1971 when the pond dried completely. During this period the water table was less than 30 cm below the present pond bottom, and the presence of large alligators would have assured that water would have remained in the pond throughout the drought. The limitation of plant growth, especially elimination of emergent vegetation, is also important because during low water, conditions in the emergent grass become seriously limiting to aquatic organisms while conditions in the open pond are still tolerable (Kushlan, 1974b).

It is apparent therefore that under natural conditions, the American alligator increased habitat diversity and maintained species richness in the southern Florida wetlands. However at present, reduction of the number of large alligators along with increased drainage and water management have altered these relationships. Canals presently serve as primary refugia in many areas, and large alligators have moved into this habitat, which is similar to the rivers and streams alligators formerly inhabited over much of their range. In areas not penetrated by canals, pre-existing ponds currently outnumber the large alligators necessary to maintain them. This, along with increasingly severe dry periods in some areas due to drainage and water control, means the increasing loss of pond habitat and their decreasing function as refugia. Although the trend is probably reversible under proper management, the importance of alligator ponds is decreasing in the artificial system now emerging in southern Florida.

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#### LITERATURE CITED

- ALLEN, R., AND W. T. NEILL. 1952. The American alligator. Fla. Wildlife 6(5):8-9, 44.  
CARR, A. 1967. Alligators, dragons in distress. Nat. Geogr. Mag. 131:133-148.  
———. 1973. The Everglades. Time-Life Books, New York.  
CARTER, G. S., AND L. C. BEADLE. 1931. The fauna of the swamps of the Paraguayan Chaco in relation to its environment. II. Respiration in the fishes. J. Linnean Soc. London 37: 327-368.  
CRAIGHEAD, F. C. 1968. The role of the al-

- ligator in shaping plant communities and maintaining wildlife in the southern Everglades. *Fla. Natur.* 41:2-7, 69-74.
- EHRENFELD, D. W. 1970. Biological conservation. Holt, Rinehart and Winston, Inc., New York.
- KUSHLAN, J. A. 1972. An ecological study of an alligator pond in the Big Cypress Swamp of southern Florida. M. S. thesis. Univ. Miami, Coral Gables, Fla.
- . 1974a. Quantitative sampling of fish populations in shallow, freshwater environments. *Trans. Amer. Fish. Soc.* 103:348-352.
- . 1974b. Effects of a natural fish kill on the water quality, plankton, and fish populations of a pond in the Big Cypress Swamp, Florida. *Ibid.*:103, 235-243.
- MCILHENNY, E. A. 1935. The alligator's life history. Christopher Publishing House, Boston.
- ROBERTSON, W. B. 1959. Everglades—the park story. Univ. of Miami Press, Coral Gables, Fla.
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**TAXONOMIC STATUS OF THE SOUTHERN RUBBER BOA, *CHARINA BOTTAE UMBRATICA*.**—The description of *Charina bottae umbratica* is based on only two specimens (Klauber, 1943), and only one brief paper on this snake has appeared after Klauber's original description (Cunningham, 1966). I therefore present data from twenty-eight specimens and provide additional information concerning the distribution, variation, and taxonomic status of this rare and protected animal.

Twenty-four of the specimens examined are from the San Bernardino Mountains, San Bernardino Co., California: Los Angeles County Museum 20264-70, Camp O-Ongo; Long Beach State University 1098-9, 6 km E of Skyforest; San Bernardino County Museum 1357, 2170, Camp Helendale and vicinity of Running Springs; LACM 27660, 0.8 km S of South Fork Campground; San Diego Natural History Museum 36549, 8 km up Fish Creek; 1 live specimen (released), Vivian Creek, 3 km E of Fallsdale; SDNHM 36011, Switzer Canyon near Lake Arrowhead; University of Kansas 152566, Camp Helendale; W. J. Fowlie, 1-6, Camp Helendale; California State Polytechnic University (2 specimens), Camp Helendale and vicinity of Running Springs. Of the remaining four specimens, three were found in the San

Jacinto Mountains, Riverside Co., California: SDNHM 40725, Marion Mt.; SDNHM 12101, Fern Valley; LBSU 1097, near Idyllwild; and LACM 2141, Newport Beach, California (not in natural range).

*C. b. umbratica* is apparently restricted to the San Bernardino and San Jacinto Mountain Ranges, although Dr. Raymond B. Cowles observed a specimen of *Charina* in the Mt. Pinos area, Kern Co., in 1935 or 1936 (pers. comm.). Furthermore, Mr. John Brode, California Department Of Fish And Game, Sacramento, found a *Charina* beneath a log next to a stream in July, 1966, Mt. Pinos, and subsequently released it without any descriptive notes being recorded. It is not known if these specimens are *umbratica*, or if they represent a southern limit for *C. b. bottae*. Based on present distribution data, *C. b. umbratica* is geographically isolated from *C. b. bottae*.

Klauber (1943) diagnosed *C. b. umbratica* as differing from other subspecies of *Charina* by the following combination of characteristics: fewer than 192 ventrals, posterior edge of frontal only slightly convex, supraoculars with blunt ends, penetrating little between frontal and parietal and reduced number of scales at midbody. He stated that as more specimens of *umbratica* became available for study, there would be overlapping among respective ventral counts for *umbratica*, *bottae* and *utahensis*. Cunningham's findings (1966) based on ten of thirty specimens of *umbratica* he collected between Running Springs and Skyforest, Lake Arrowhead, 5 km SE of Cedar Glen, the headwaters of Sheep Creek and of Shake Creek, and 13 km E of Barton Flats, agree favorably with mine. Cunningham (1966) gave a mean of 190.90 for ventrals, and a mean of 38.80 for scale rows at midbody. My data indicate a mean ventral count of 191.43 (Range 182-217, SD 6.27, SE 1.19, Coef. Var. 3.28%, N = 28) and a mean scale row count of 38.71 (Range 32-42, SD 1.64, SE 0.31, Coef. Var. 4.24%, N = 28). In *C. b. bottae*, Klauber (1943) and Cunningham (1966) gave means of 205.02 and 206.67 for ventrals, 46.43 and 46.93 for scale rows at midbody (data include two samples including both sexes). In *C. b. utahensis*, Klauber (1943) and Cunningham (1966) gave means of 204.80 and 202.33 for ventrals, 41.77 and 43.00 for scale rows at midbody (data include two samples including both sexes).

The most important diagnostic characters