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Environmental Effects on a Coastal Population of Gopher Tortoises

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ABSTRACT.—**Gopher tortoises (*Gopherus polyphemus*) typically occur in upland xeric habitats, where long-term stability is thought to be required for population persistance. The southernmost population on Cape Sable, Florida, occupies 113 ha of unstable coastal dunes. This isolated population is relatively dense, estimated at 11.3 tortoises/ha, and consists of over 1200 tortoises. Burrows are randomly distributed over the coastal grassland habitat. The size distribution of burrows suggests the occurrence of larger animals than in other populations studied, probably owing to the long-term absence of human predation. Population density seems to have increased substantially in the 16 years since the last hurricane passed over the area. Environmental conditions, particularly storms and drought, may explain the recent population trend, size structure, and distribution of this coastal population.**

The gopher tortoise (*Gopherus polyphemus*) is widely distributed along the southeastern coastal plain of North America. Its population core is in southern Alabama and Georgia and in northern and central Florida, where it inhabits inland xeric habitats, especially pine scrub (Ernst and Barbour, 1972). Nearly all published information on the population ecology and status of gopher tortoises is from these upland habitats (Auffenberg and Iverson, 1979; Alford, 1980; Iverson, 1980; Auffenberg and Franz, 1982; Landers et al., 1982). Auffenberg and Franz (1982) noted that tortoises are generally absent or scarce in low-lying areas near the coast, particularly in the poorly drained southern half of the Florida peninsula. Gopher tortoises do occur in coastal dune habitats (Auffenberg, 1978), although little is known about their ecology there. The southernmost population occupies the coastal beach dunes of Cape Sable, Florida (Fig. 1).

The gopher tortoises of Cape Sable are disjunct from currently and previously occurring populations further north. The population is also notable in its being protected from human predation for decades, owing to its location in Everglades National Park. The dune environment of Cape Sable is unstable because of periodic tropical storms, a factor that may affect tortoise population characteristics. In this respect Alford (1980) has suggested that long-term habitat stability may be required for the persistence of tortoise populations. The literature contains only the barest mention of the existence of the Cape Sable population (Carr and Goin, 1955; Auffenberg, 1978) and no analysis of its status or population structure. The purpose of the current study was to analyze the size, structure, and distribution of this isolated island population of gopher tortoises and to consider possible environmental factors affecting population characteristics.

STUDY AREA

Cape Sable (Fig. 1) is the southwestern tip of the Florida peninsula. Its general characteristics have been described by Craighead (1971). The cape is isolated from the mainland by Whitewater Bay and by a canal between Whitewater and Florida Bays at the developed area of Flamingo. Sandy beaches of marl,

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shell, and some quartz occur along the shorelines of East, Middle, and Northwest Capes. Middle and East Capes are separated from the rest of Cape Sable by Lake Ingraham and canals connecting the lake to tidewater. The spatial sequence of vegetation away from the beach (Fig. 2) is similar on all three capes. Inland from the beach is a xeric coastal prairie grassland, the nearly exclusive habitat used by gopher tortoises on East and Middle Capes. The prairie, covering a series of low dunes and swales, is composed of *Lantana involucrata, Schizachyrium semiberbe, Andropogon virginicus, Boerhavia repens,* and clumps of *Cocos nucifera, Sabal palmetto,* and *Agave* sp. Inland, on higher elevations, are stands of hardwood hammock forest containing well-developed trees of *Bursera simaruba, Piscidia piscipula, Ficus aurea,* and tall *Yucca aloifolia.* We found few burrows on the edge of the hammock forest on Middle Cape. Beyond the hammock are mangrove swamp forests, dominated by *Rhizophora mangle,* stretching to Lake Ingraham. The grassland occupies more area on Middle Cape than on Northwest Cape or East Cape. As a result of a larger catchment area, the groundwater of Middle Cape is fresh, potable water occurring 50 m from the beach even during extreme droughts (Russell 1971). On Northwest Cape, fresh groundwater is lost during droughts.

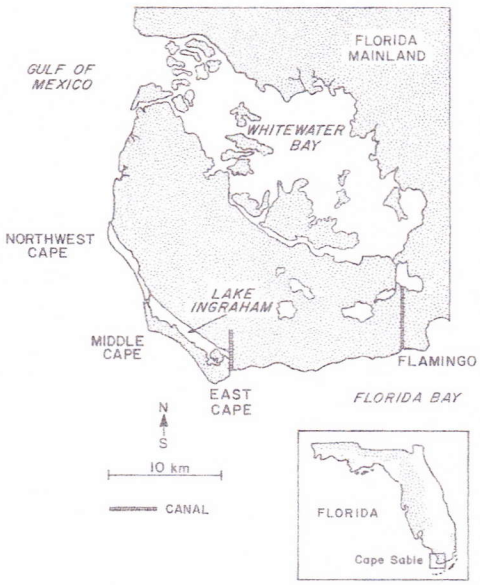

FIG. 1. Map of Cape Sable, Florida. Insert is a map of Florida showing the location of Cape Sable and the range of the gopher tortoise (stippling).

METHODS

All upland areas on the three capes were searched for gopher tortoise burrows. Because tortoises occurred only in prairies, our quantitative study was confined to that habitat. The area covered by prairie vegetation was determined from aerial photographs using dot grids. The census technique was modified from that of Auffenberg and Franz (1982). Sixty 7-m wide transects were walked from the beach inland to the tree line and back to the beach. Because distance to the tree line varied, transect lengths differed. The census team counted all burrows within the transect boundaries. Five persons walked those transects longer than 100 m, whereas shorter transects were adequately covered by two people. Following Auffenberg and Franz (1982), we classified burrows as active (signs of recent use), inactive (leaves, twigs in hole, no signs of recent use), or abandoned. The first two are considered in population totals. The distance of each burrow from shore was recorded. The transects covered 13.8% of the total available habitat of prairie vegetation. The census was conducted on 22–23 August 1979 on Middle Cape and 18 November 1981 on East Cape. Studies elsewhere have shown that on the average 38.6% of all unabandoned burrows are unoccupied (Auffenberg and Franz 1982). Lacking similar information for the study population, we applied their correction factor of 0.614 turtles/burrow to the count of active and inactive burrows in order to esti-

FIG. 2. Aerial view of Middle Cape, Cape Sable, Florida, showing tortoise habitat, coastal prairie grassland with scattered trees. Mangrove swamp forest surrounds Lake Ingraham, in the background, and also occurs in a forested patch near the point of the cape. Hardwood hammock forest is located along the inland edge of the prairie.

mate the number of tortoises in the population. Further information can be found in a report available from the South Florida Research Center (Kushlan and Mazzotti 1982).

A permanent plot of 1.45 ha was established in August 1979 on Middle Cape. All burrows in the plot were counted, marked, and measured (width and height) below the mouth at the point the burrow narrows. The plot was recensused on 8 November 1980 and 22 February 1982. In 1982 we also measured burrow width as far into the burrow as possible to correspond to the method used by Alford (1980). For conversion of burrow width to carapace length, we used the equation $\log_{10}Y = 0.879 \log_{10}X + 0.149$ derived by Alford (1980). Dispersion of burrows was analyzed using the nearest neighbor method (Poole 1974).

Data from the plot were also used to evaluate the accuracy of the transect census technique. Transects run within the plot produced an estimated density of 51.82 burrows/ha, whereas the plot actually contained 51.03 burrows/ha. This comparison inspires confidence that the transect data were adequate to estimate tortoise burrow density over the entire study area.

RESULTS

Extensive survey work showed that gopher tortoises were confined to Middle and East Capes (Fig. 1). The prairie habitat on these capes was 113.3 ha in extent. On the census of 60 transects covering 13.8% of occupied area, we located 253 active and inactive burrows. From this, we calculated the cape contained 2077 burrows at a density of 18.3 burrows/ha, and we estimate the pop-

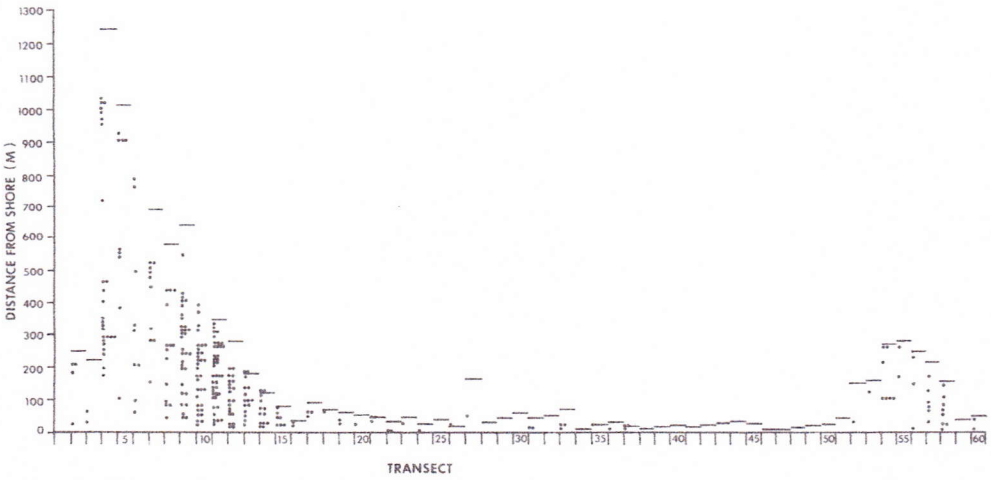

FIG. 3. Distribution of gopher tortoise burrows along each transect. Sixty transects were run perpendicular to the shoreline at intervals from Middle Cape to East Cape. The horizontal axis is the shoreline, straightened for clarity. Transect No. 1 was at the point of Middle Cape shown in Fig. 2. Transect 1 to 15 were on Middle Cape, 51 to 60 were on East Cape, the rest in between. Dots show location of burrows away from the shoreline along each transect. The horizontal lines show the location of the inland edge of the prairie and beginning of the hammock forest.

ulation to be 1275 tortoises at a density of 11.3 tortoises/ha.

Burrows were scattered throughout the dune area, from the foredune to slightly beyond the tree line edge of hammock forest (Fig. 3). We found only three burrows within 10 m of the beach, suggesting tortoises avoided digging burrows in areas subject to flooding from overwash. Tortoises were active in this area though, as shown by the presence of scat and trails. The dispersion of burrows within the study plot in August 1979 was random ($R = 1.09$, $Z = 1.5$, $N = 73$), but there did appear over the entire habitat to be a concentration of burrows on ridges with fewer in the intervening swales. There was no apparent preferred use by tortoises of vegetation types within the prairie; some burrows were located under trees.

The three censuses conducted on the study plot provided a complete count of burrows there. In 1979 we found 74 active and inactive burrows; in 1980 we found 84; in 1982 we found 86. These three complete counts imply that the population on the plot may have been increasing during the study period.

Some idea of the relative size structure of the population can be obtained from our measurements of burrows (Table 1). The presence of small burrows less than 15 cm wide suggests that recruitment is occurring within the population. The smallest burrow was 6.0 cm wide. These were made by young tortoises, although probably not by hatchlings (Alford, 1980; Arata, 1958). Most

TABLE 1. Distribution of the widths of the mouths of gopher tortoise burrows in a 1.45-ha study plot on Middle Cape.

Size range (cm)	August 1979	February 1982
5–9.9	4	9
10–14.9	7	13
15–19.9	3	3
20–24.9	5	4
25–29.9	11	14
30–34.9	11	26
35–39.9	22	13
40–44.9	6	1
45–49.9	5	3

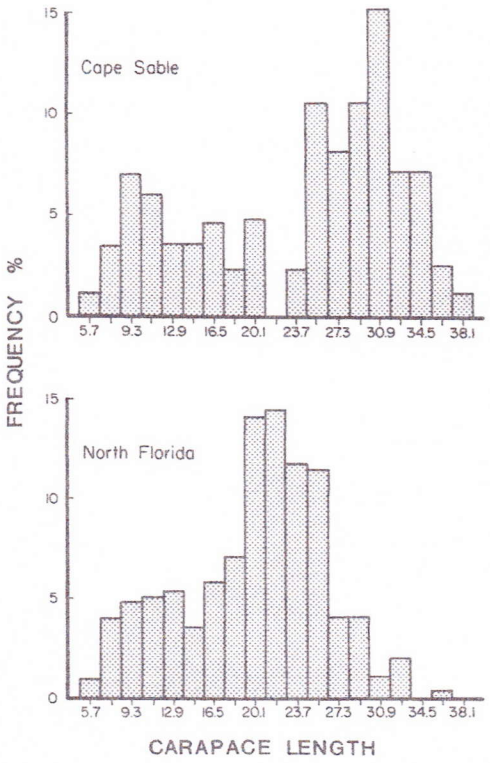

FIG. 4. Frequency distribution of calculated carapace lengths (in centimeters) of the gopher tortoise population on Cape Sable contrasted with one in north Florida (Alford, 1980). Size classes are 1.8 cm wide matching those of Alford (1980).

burrows were between 25 and 40 cm wide.

Alford (1980) determined the relationship between burrow width and carapace length of gopher tortoises. In 1982, we measured burrow width in a way comparable to Alford's and so used his relationship to generate a size-frequency distribution for the population segment in the study site (Fig. 4). The resulting distribution shows a predominance of animals in the 25 to 35 cm carapace length classes, with good representation of smaller animals.

In 1982 and 1983, burrows were examined for the presence of commensal animals. In 1982 we excavated two burrows and found slugs and a whip scorpion. To investigate further, A. Beck and J. Butler took vacuum samples (Butler and Gibbs, 1982) of 26 burrows finding spiders and greenhouse frogs (*Eleutherodactylus ricordi*).

In order to determine whether archeological evidence existed for the early occurrence of gopher tortoises on Cape Sable, G. P. Fischer (pers. comm.) examined records of material collected in two Indian middens on Cape Sable. He was able to find no report of turtle remains.

DISCUSSION

We estimate that the southernmost gopher tortoise population, located on Cape Sable, Florida, includes in excess of 1200 individuals in 113 ha. This population had a within-colony density of 11.3 tortoises per hectare of habitat, a density relatively high compared to other populations (J. Diemer, J. Butler, pers. comm.). T. Logan (pers. comm.) found that tortoise populations on 17 federally managed areas in Florida had densities ranging from 0.3 to 11.9 tortoises per hectare of habitat. Our data confirm that, of natural habitats, coastal areas tend to have the highest tortoise densities (Auffenberg and Iverson, 1982; J. Diemer, pers. comm.).

The gopher tortoise population on Cape Sable is entirely isolated from others, but it could have derived naturally by rafting from Gulf Coast populations or by rafting down the Everglades from inland populations along the coast (Fig. 1). The nearest coastal population was on Marco Island, 100 km NW. Gopher tortoises occur, at least sporadically in the pine forest 82 km inland. Recent observations were in 1955, 1957, 1960, 1979, and 1981 (Everglades National Park files). The infrequency of observations indicates that these animals had been released in the park rather than being remnants of a naturally occurring population.

It has been suggested that gopher tortoises may have been introduced onto Cape Sable by man (McKinney 1970). Tebeau (1968) in discussing the history

of human occupation of the cape, noted that it was probably used only sporadically by Indians. The first non-Indian occupation of the site was in 1838 during the Seminole War when a temporary fort was constructed on East Cape. Records exist of occasional transient settlement, farming, and cattle ranching in the 19th century and of a coconut plantation that was finally destroyed by the hurricane of 1935. It is possible that any of these human occupants of the cape may have introduced tortoises there. The cape has been unoccupied since the national park was established in 1947.

McKinney (1970) argued for introduction because his excavation of five burrows failed to produce any commensal animals, including any obligate commensals characteristic of gopher tortoise burrows (Young and Goff, 1939). He suggested that their absence indicated that the tortoises were originally transported to the cape by man. Although we were able to find nonobligate commensals, the Cape Sable burrows were very barren of such animals compared to those in other parts of the state (D. Beck, pers. comm.). Considering that storms, which periodically flood the cape (Craighead, 1971), could easily kill obligate commensal invertebrates, their absence on Cape Sable provides little information on the tortoises' history there.

The lack of tortoises on Northwest Cape has been cited as evidence of their introduction after the construction of the canal separating Northwest and Middle Capes (Robertson, 1957). This canal was dug in the early 1920's (Tebeau, 1968); however, Simpson (1920) reported that tortoises were present on Cape Sable prior to 1920. It is likely that the tortoises absence on Northwest Cape may be due to habitat differences, perhaps related to the lack of persistence of a fresh ground water lens during drought. In any case turtles occurred on Cape Sable prior to 1920, but how much earlier is not known. Barring the fortuitous discovery of datable archeological remains, the question of the origin of this population remains unsettled. We note, however, that occupancy of coastal beaches by gopher tortoises is not atypical (Auffenberg and Franz, 1982) and that Cape Sable represents the southernmost suitable habitat.

The population was rediscovered on Middle Cape on 9–10 October 1949 by W. Dilley, R. O. Woodbury, and J. B. Earle. Subsequently, on 2 March 1950, J. Moore (1953, pers. comm.) found a number of burrows and signs of activity on East Cape. Tortoises were later observed in 1951, 1952, and 1955. In this period, the population must have been considerably smaller, or at least less noticeable than at present, because Albert Schwartz (pers. comm.) spent several days camping on Middle Cape in the 1950's but remained unaware of their existence when he assembled his monograph on south Florida reptiles (Duellman and Schwartz 1958). Tortoises were present on both East and Middle Cape in 1960 and 1961, proving their survival after Hurricane Donna in 1960. On 2 April 1966, after Hurricane Betsy, E. T. Christensen (memo Everglades National Park files) censused 81 hectares and found 0.2 burrows/ha (0.12 tortoises/ha). From this history it appears that the population was present but small in the 1950's and 1960's. It has increased in subsequent years, the present population density on Middle Cape being 90 times that recorded in 1966. The population on the study plot also seems to be increasing, as evidenced by the number of burrows increasing by 16% between August 1979 and January 1982. Although the higher number of burrows could have been caused by immigration from outside the plot (McRae et al., 1980), the increase in small burrows (Table 1) suggests that reproduction was the primary factor. A rapid population increase since 1966 may have been possible because of the large clutch size in

south Florida compared to more northern areas (Iverson, 1980; Landers et al., 1980).

The population has a relatively high proportion of larger, presumably older animals, the predominance of animals being 25 to 35 cm long (calculated carapace length). This population includes larger animals than Alford (1980) found in northern Florida, where most animals were 19 to 27 cm long (Fig. 4). Alford interpreted his data as demonstrating a relatively high number of large tortoises in his population. He stated that the likely explanation was a slowing in the development rate of older tortoises, leading to the bunching of older cohorts. On Cape Sable, tortoises are free from human exploitation, and even older age classes seem to be represented (Fig. 4). Information on the actual, rather than calculated, size distribution of Cape Sable tortoises would allow further consideration of this point.

We believe that the population on Cape Sable is affected primarily by environmental conditions. Seasonal drought may adversely impact tortoises, especially where fresh water does not persist during the dry season, as on Northwest Cape. Rainfall floods burrows in swales in the summer; Moore (1953) reported how raccoons use such water-filled holes for drinking. Flooding of burrows would affect details of burrow placement, even if it did not kill tortoises directly. Storms may have an especially profound effect on population size and distribution. The low populations of the mid-1950's followed hurricanes in 1947 and 1951. Tortoises seem to have survived the hurricanes of 1960 and 1965, in relatively small numbers. After the 1965 storm, Christensen found the tortoises 60 to 150 m back from the beachfront, with the greatest number of holes 150 m inland, close to the hammock ridge. This distribution was very different than at present (Fig. 3). The burrow distribution found in 1966 suggests that tortoises closer to the beach on lower ground did not survive the hurricane. It is possible that the recent population expansion may have coincided with the latest interhurricane period.

Storms may also account for the current size structure of the population. Although growth rates of Cape Sable tortoises have not been studied, information exists for other populations. Growth rates of gopher tortoises are complex, varying with age, nutrition, and latitude (Landers et al., 1982) and are relatively higher in more southerly populations (Landers et al., 1982), presumably also on Cape Sable. If Alford's (1980) estimates of growth rates in Florida are not greater than those of Cape Sable tortoises, members of the modal size class (30.9 cm mid-point, Fig. 4) would be over 15-years old and would have survived the last major hurricane in 1965. The dip centered in the 22 cm size class (Fig. 4) may represent animals lost in that hurricane.

Cape Sable is part of Everglades National Park, and the population is thereby protected from the hunting that occurs elsewhere in Florida. Thus, the most severe threat to the tortoise seems to be from natural causes, especially hurricanes. The Cape Sable coastal system of dunes and swales of successive deposition was in large part shaped by such storms (Craighead, 1971). Although Alford (1980) concluded that long-term habitat stability seems to be needed for tortoise survival, coastal beaches are inherently unstable. On Cape Sable, the tortoise population appears to have survived storms, but in reduced density. If inter-colony movement were low under the best of conditions (Alford, 1980), recolonization of isolated population centers such as Cape Sable would be an unlikely event. Thus, local extinction of the population on coastal beaches of Cape Sable may be an eventual possibility, and at any time its numbers and structure are determined

by the recent history of environmental conditions.

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