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# GOPHERUS BERLANDIERI IN SOUTHEASTERN TEXAS

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# *GOPHERUS BERLANDIERI* IN SOUTHEASTERN TEXAS

Walter Auffenberg and W. G. Weaver, Jr.[1]

Synopsis: *Gopherus berlandieri* populations on isolated clay dunes near the mouth of the Rio Grande were studied intermittantly from 1961 to 1967. Reproduction, growth, habitat, movement, activity, shelter, food, and predation were investigated. The most important contribution of the study is the demonstrated interpopulational behavioral variability in shelter construction and use, activity range, and food preference. The geological and vegetational histories of the habitats of each population are correlated with the behavioral differences observed.

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[1] The Bulletin of the Florida State Museum has included several contributions on fossil tortoises by Walter Auffenberg, Curator in Herpetology, and on snake anatomy by W. G. Weaver, former graduate student, University of Florida. Manuscript received 3 August 1967.

Auffenberg, Walter and W. G. Weaver, Jr. 1969. *Gopherus berlandieri* in southeastern Texas. Bull. Florida State Mus., Vol. 13, No. 3, pp. 141-203.

## INTRODUCTION

The present contribution represents a portion of the studies initiated by Auffenberg on the systematics, comparative ecology, and behavior of the genus *Gopherus*, of which the living populations are believed to comprise two distinct species groups. *Gopherus polyphemus*, a member of one of these groups (*G. polyphemus* and *G. flavomarginatus*), is currently being studied in Florida. Comparative data for members of the other species group (*G. agassizi* and *G. berlandieri*) are largely lacking. Preliminary investigations of the ecology and habits of both *G. agassizi* and *G. berlandieri* were initiated to select one of these species for more detailed studies. A survey of different populations of *G. agassizi* within its range (W. A. field notes, 1962, 1963, 1964) showed so much variation in the ecology and habits of this species that to pick a typical population for intensive study is difficult. We know that Woodbury and Hardy's excellent study (1948) represents a rather unusual situation, typical only of a restricted area at the northern part of the species range, and including only those populations living under rather specific conditions of soil and climate. The frequency of such instances of behavioral adaptations by populations of all the species of *Gopherus* has stimulated us to consider the vegetational, climatic, and geological facets of the study area in more detail than is usual in such studies.

Preliminary studies throughout the range of *G. berlandieri* indicated that this species is considerably less variable in both ecology and habits than *G. agassizi;* thus we chose *G. berlandieri* for intensive study. We found population densities near Brownsville, Texas higher than in any other area investigated, and so selected this region as the major study area. At this point the preliminary survey quickly developed into a long term project with definitive goals. These were to obtain appropriate data for comparing behavioral and ecological aspects of the biology of *G. berlandieri*, as a representative of one species group, with those of *G. polyphemus* as a representative of the other group. Populations of *G. agassizi* and *G. flavomarginatus* are to be studied similarly at a later date; some preliminary data have already been accumulated on these two species.

The authors and their associates spent a total of 157 man days in the field studying *G. berlandieri* after the project was initiated in August 1961. Intensive study in the Brownsville area was begun in May 1962 and continued in November 1963, July 1964, July and August 1965, April 1966, June 1966, August 1966, and June 1967.

Since 1961 one or the other of the authors has examined the habitat of *Gopherus berlandieri* along almost the entire periphery of its range. Field observations have been made from Aransas Pass westward to San Antonio, southward to Eagle Pass and Laredo, and thence to Monclova, Monterrey, Ciudad Victoria, and Tampico, Mexico; W. G. Weaver did considerable additional work on behavior and ecology at Sinton, Texas.

During the study several aspects of the biology of *G. berlandieri* were investigated, but this report presents only those data bearing on the movement, ecology, and certain morphological characteristics of several essentially isolated populations near Brownsville. Where pertinent, data from populations in other parts of the range are included. Weaver plans to publish separately all data pertaining to combat and courtship.

## ACKNOWLEDGEMENTS

Without the aid of many individuals and institutions this study could not have been completed. In particular we wish to acknowledge the receipt of living specimens from several parts of the range from Bernardo Medina, Brownsville, Texas; Michael Sabbath, University of Texas; and the late J. M. Wilks, formerly of the Bob and Bessie Welder Wildlife Refuge, Sinton, Texas. The University of Florida Herbarium was exceedingly helpful in the identification of plant material. The American Philosophical Society provided the senior author with a grant to initiate a study of *Gopherus* (Johnson Fund, 406). Support during the subsequent period of research was provided by the National Science Foundation (NSF GB1413 and 3738). Facilities and some financial assistance were supplied continuously by the Florida State Museum. We also wish to acknowledge the support offered the junior author by the Welder Wildlife Foundation during the summer of 1965. The Graduate School, University of Florida, supported the important terminal trip to the study area in August, 1966.

In particular we wish to thank Mr. A. B. Westbrook, City Manager, Brownsville, Texas for making his property available for our studies and for extending every courtesy during our visits to southeastern Texas.

## AREA CHARACTERISTICS

### REGIONAL FEATURES

TOPOGRAPHY. — The study area lies in the southeastern quadrant of Cameron County, Texas, near the middle of the Tamaulipan Biotic Province (Blair, 1950, 1952). Specifically it is in the area known as Jackass Prairie — a broad, treeless, saline plain dominated by coarse, bunchy sacahuista *(Spartina)*. This plain stretches 10 miles inland north of the present natural levees of the Rio Grande. The most studied tortoise population lives on the Loma Tio Alejos, a small,

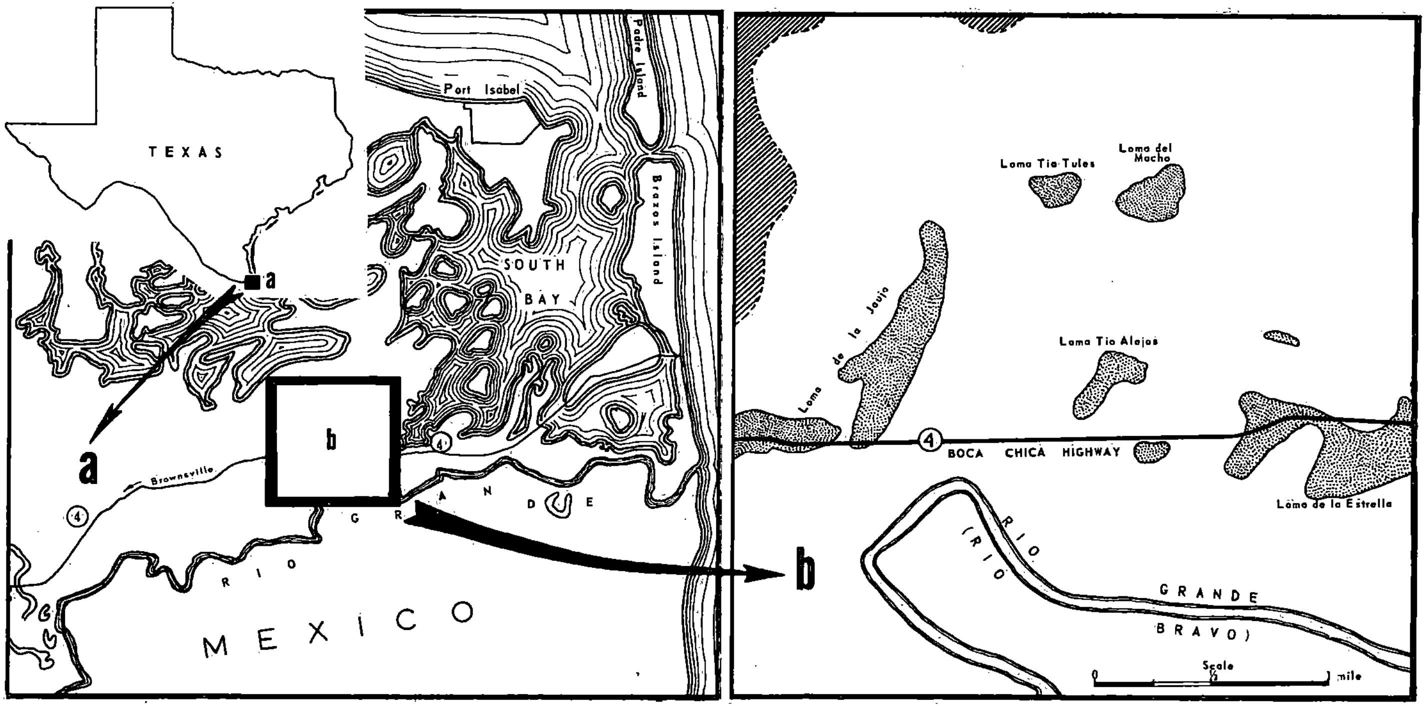


FIGURE 1. Location of study area.

isolated hill (loma) 400 feet north of the Boca Chica Highway (Texas Highway 4) at its closest point; 14.5 miles east of the center of Brownsville and 8.2 miles west of the Atlantic Coast of Boca Chica Beach (Fig. 1). Completely surrounded by seasonally innundated brackish water flats, the loma rises from 5 to 26 feet above mean sea level at its highest point with a rather steep erosional scarp from 10 to 20 feet above mean sea level around most of its periphery. A gently inclined outwash plain lies between the base of the scarp (10 ft. el.) and the outer edge of the loma (5 ft. el.). The loma top is rather flat, sloping to the southeast from about 26 to 20 feet above mean sea level. Its greatest length is 1800 feet and its shape from above is roughly triangular (Fig. 2).

The loma is separated from other similar rises in the same plain by intervening flats. The nearest surrounding rises are the Loma de la Estrella, 2000 feet ESE; the Loma de la Jauja, approximately 3000 feet W; and two smaller lomas, Tia Tules and del Macho, 3500 feet N (Fig. 1). *Gopherus berlandieri* occurs on all these rises, though population densities vary from one to the next. Because of the ecology of the intervening flats, genetic interchange between these populations is probably rare, if it occurs at all. Studies were also conducted on a number of other lomas in the area, most of them very similar to the Loma Tio Alejos except as noted below.

Soil. – The predominant soils of the deltaic plain near the mouth of the Rio Grande are halomorphic, developed where evaporation exceeds rainfall in poorly drained tidewater areas (Thorp and Smith, 1949).

The poor drainage, poor aeration, high salt content, recurrent submersion, and high insolation on the vegetated parts of the flats all serve to produce an intrazonal soil of a dark gray to yellowish Solonchak type. On the nonvegetated, wind-deflated, playa portions of the flats the soil is of an azonal, dark brown to gray, alluvial type, originating from silts transported by the Rio Grande and its tributaries and deposited on the flats during flood conditions. Salinization of these sediments develops as a result of intermittent tidal flooding and evaporation. On the lomas themselves the soil is also a halomorphic, azonal type, although its deposition is eolian. Farther inland the major soil is Rendzina. This calcimorphic soil is developed mainly from a limestone parent material (Brambila, 1957).

Climate. – The climate of the lower Rio Grande Valley is humid and subtropical, characterized by relatively warm temperatures in all seasons. Winters are usually short and mild. High summer temperatures occur for long periods with readings near 100° F. common. Norquist's (1941) synopsis of weather data compiled for more than 40 years at the Brownsville airport includes the following: mean temperature ranges from 59.8° F in January to 83.6° F in July;

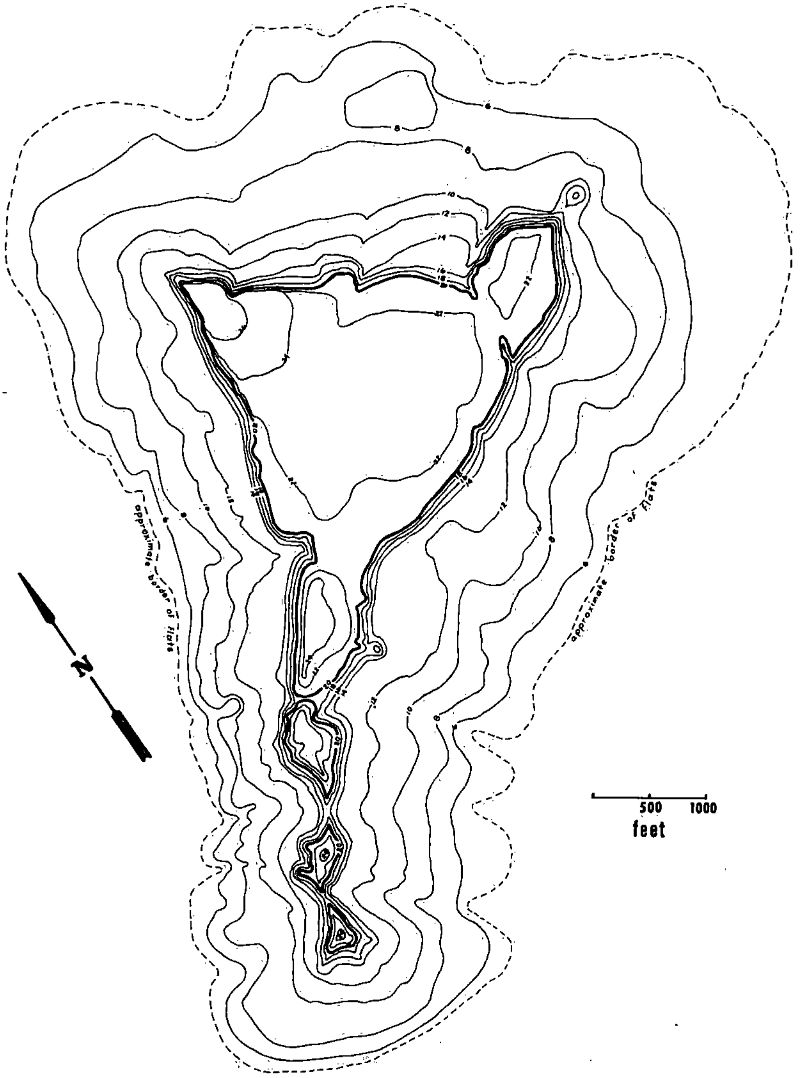


**Figure 2.** Topography of the Loma Tio Alejos, southeastern Cameron County, Texas. The major study site is typical of the clay dunes in this region. Contour interval = 2 feet.

mean annual maximum temperature 98°, mean annual minimum 30°; highest temperature ever recorded 104°, lowest 12°; mean date of earliest killing frost December 26, latest January 30; mean length frost free period 330 days. Some years are completely free of frost. The mean July daytime temperature 1 inch above the surface at the Loma Tia Alejos is 108.4° in the shade.

The mean annual precipitation in Brownsville is 26.3 inches. No records are available for the eastern end of the Boca Chica Road, but the study area is presumed to have as much, or perhaps more rain than at the Brownsville airport. Though rainfall is erratic, most of it normally falls in September (5.2 inches). In May, June, July, August and October average rainfall varies from 2 to 3 inches. For the remaining months the averages are less than 2 and more than 1.25 inches. The average spring precipitation (March-May) is 5.6 inches, summer (June-August) 7.2, fall (September-November) 9.0, and winter (December-February) 5.3 inches. The average relative humidity at the airport at 8 AM in January is 83%; in July 90%; at noon in January 67%, in July 58%; at 8 PM in January 76%, in July 70%. The study area is undoubtedly slightly drier than this, and the potential evaporation ratio is certainly lower than 2.80 and higher than 2.00. The prevailing winter winds are northerly; those of the summer southeasterly.

VEGETATION. — The vegetation of the lower part of the Rio Grande Valley represents a southern extension of the semiarid, middle latitude steppe characteristic of much of the western part of the Gulf Coastal Plain. In the Holdridge life zone system the area is called warm temperate subhumid dry forest, though edaphic features place it close to thorn woodland. The present vegetation consists mainly of dense shrubs, most of them thorny. This frost-conditioned grassland and brush, which Weaver and Clements (1938), call the Coastal Prairie, they describe as "a chaparral-mesquite post climax of a grassland climax," a cumbersome definition based on their assumption that the local abundance of short grasses is a result of their climatic dominance. It is now known that recent overgrazing has favored the short grasses over taller grasses (Box, 1961). Kendeigh (1961) places the region within the *Aristida-Bouteloua* association, which he describes as the most arid of grasslands. His view that overgrazing and fire control are responsible for the conspicuousness of mesquite and cactus is shared by most ecologists familiar with the area. Weaver and Clements (1938) regard the extension of the mesquite brushland of southern Texas and northeastern Mexico in

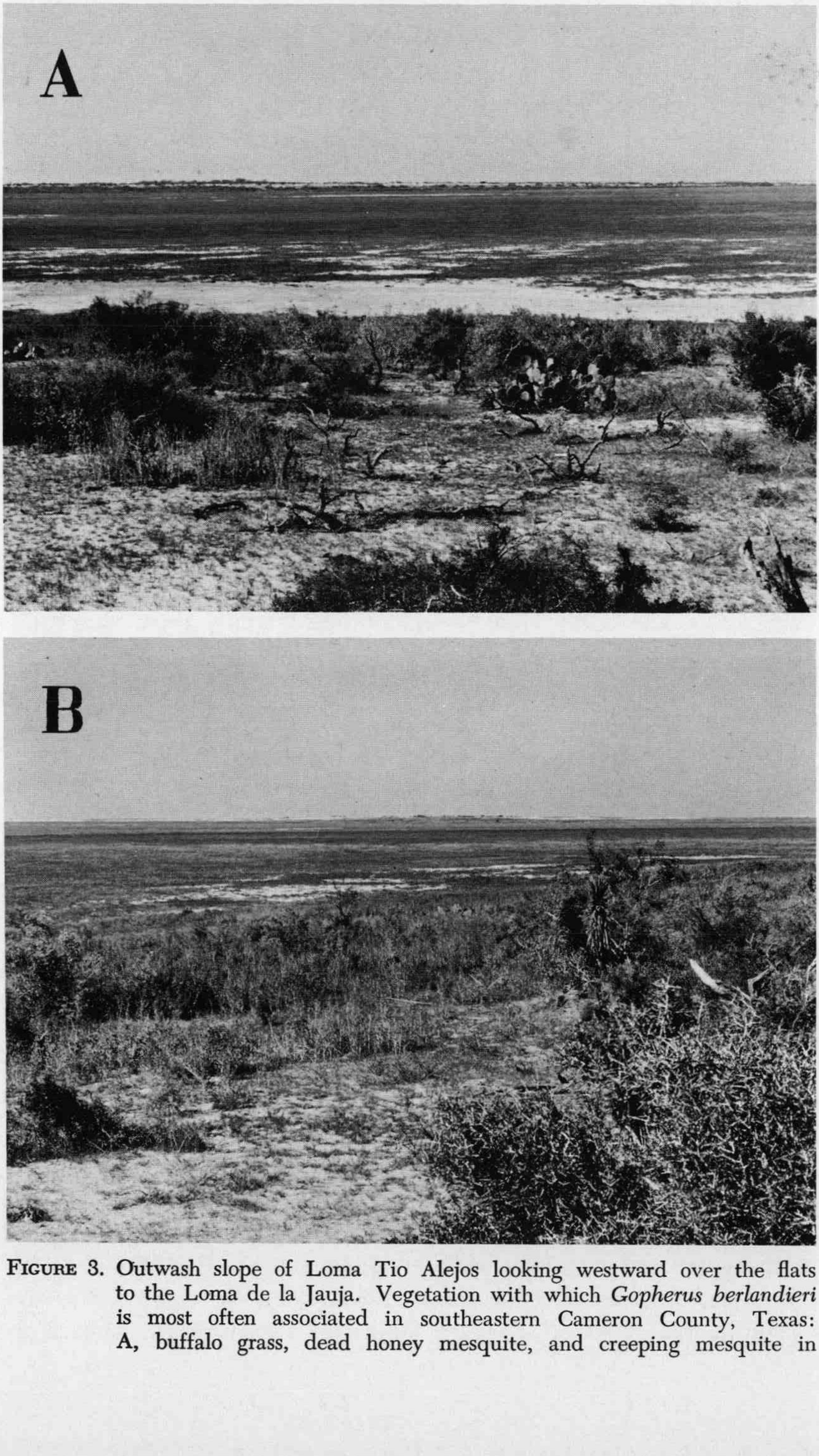
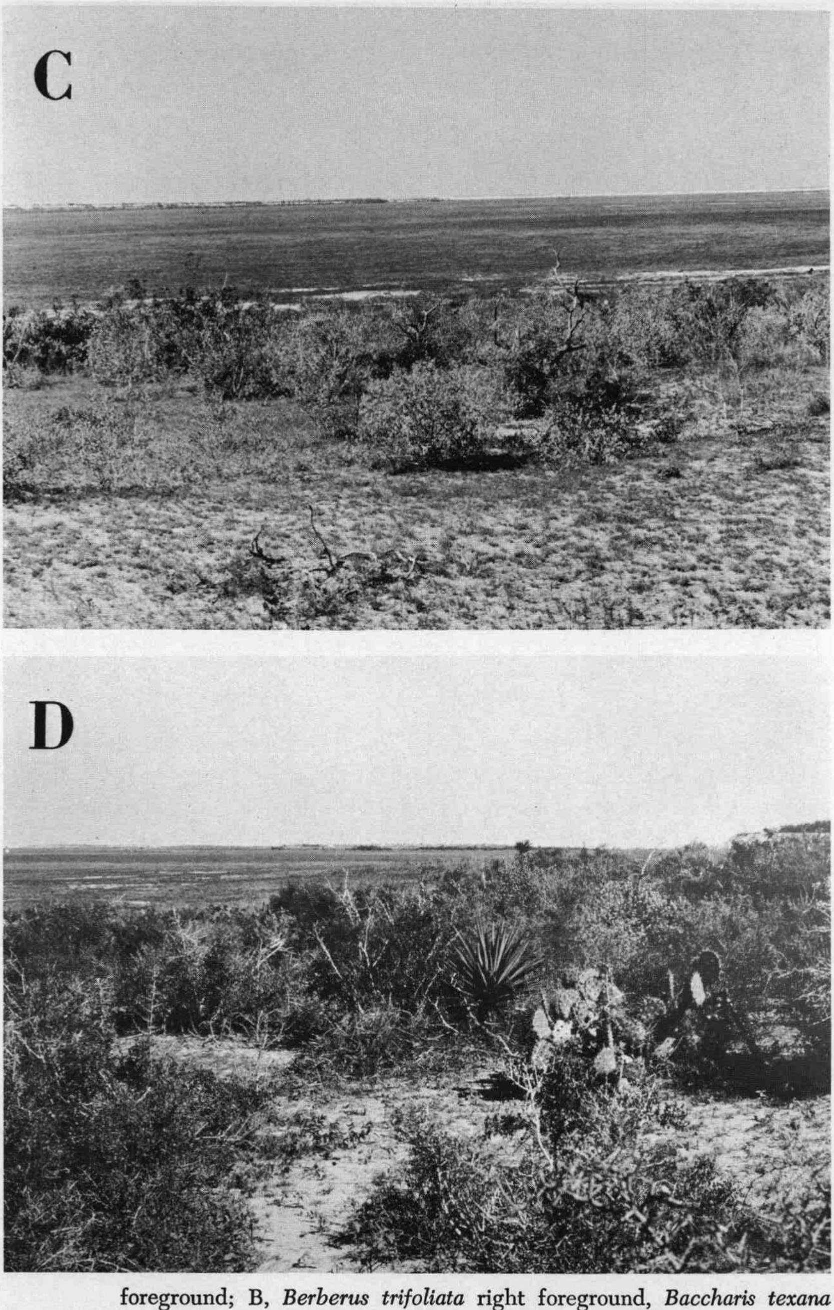


FIGURE 3. Outwash slope of Loma Tio Alejos looking westward over the flats to the Loma de la Jauja. Vegetation with which *Gopherus berlandieri* is most often associated in southeastern Cameron County, Texas: A, buffalo grass, dead honey mesquite, and creeping mesquite in



foreground; B, *Berberus trifoliata* right foreground, *Baccharis texana* in middle; C, buffalo grass in foreground, *Leucophyllum* and dead honey mesquite in middle; D, mixed, open bush.

the historical period as a pre-climax associes. Regardless of the complexities of definitions reflecting the presumed ecological development of the present vegetation, early explorers and naturalists described the region as a vast grassland, with trees only along the waterways (Havard, 1885).

Several different but related vegetational associations occur on the lomas of the Jackass Prairie. To some extent they reflect successional stages. The flora of the Loma Tio Alejos area is typical of the plain and is described below (Figs. 3-6).

The most extensive plant cover on the flat loma top is a southern Texas chaparral association, consisting of several species of thorny shrubs and low trees. Dominant woody species include lotebush *(Condalia obtusifolia)*, honey mesquite *(Prosopis glandulosa)* and huisache *(Acacia farnesiana)*. Prickly pear *(Opuntia lindheimeri)*, tassajillo *(Opuntia leptocaulis)*, lime prickly ash *(Xanthophylum fagara)*, and yucca *(Yucca traculeana)* grow along the edges of the thick brush and in open patches. The association has few forbs. Grasses, which are most abundant on the edges of the thick cover, include three-awn grass (*Aristida* sp.), short grass (*Bouteloua* sp.), and sand bur *(Cenchrus* sp.*)*. Parts of the loma top are more open, with an extensive grass cover dominated by buffalo grass *(Buchloe dactyloides)*.

The steep, eroding slope of the loma is a zone of an almost bare sandy clay, variable in width, and supporting only a few woody plants or shrubs such as creeping mesquite *(Prosopis reptans* var. *cinerascens)* and prickly pear. Rapid runoff and low infiltration rates on the slopes prevent most plant growth.

At the base of the erosional slope a gently sloping outwash plain extends to the flat. Grasses are more extensive on the higher parts of this slope than on top of the loma. The dominant grasses are sand bur, curly mesquite *(Hiliaria berlanderi)* and buffalo grass (Fig. 3). On the west side of the loma the outwash slope is broken by brush clumps similar in composition to those of the loma top. On the southeast side the open brush association is provided with an understory of windmill grass *(Chloris verticillata)*, 3-awn grass, and sand bur. With the exception of the northern end of the loma, the middle portion of the outwash is covered with brush clumps composed of lime prickly ash, granjeno *(Celtis pallida)*, honey mesquite, lotebush, huisache, agarito *(Berberis trifoliata)*, prickly pear, tassajillo, and creeping mesquite (Fig. 4). *Leucophyllum frutescens* occurs in mixed and nearly pure stands in several places on the lower part of

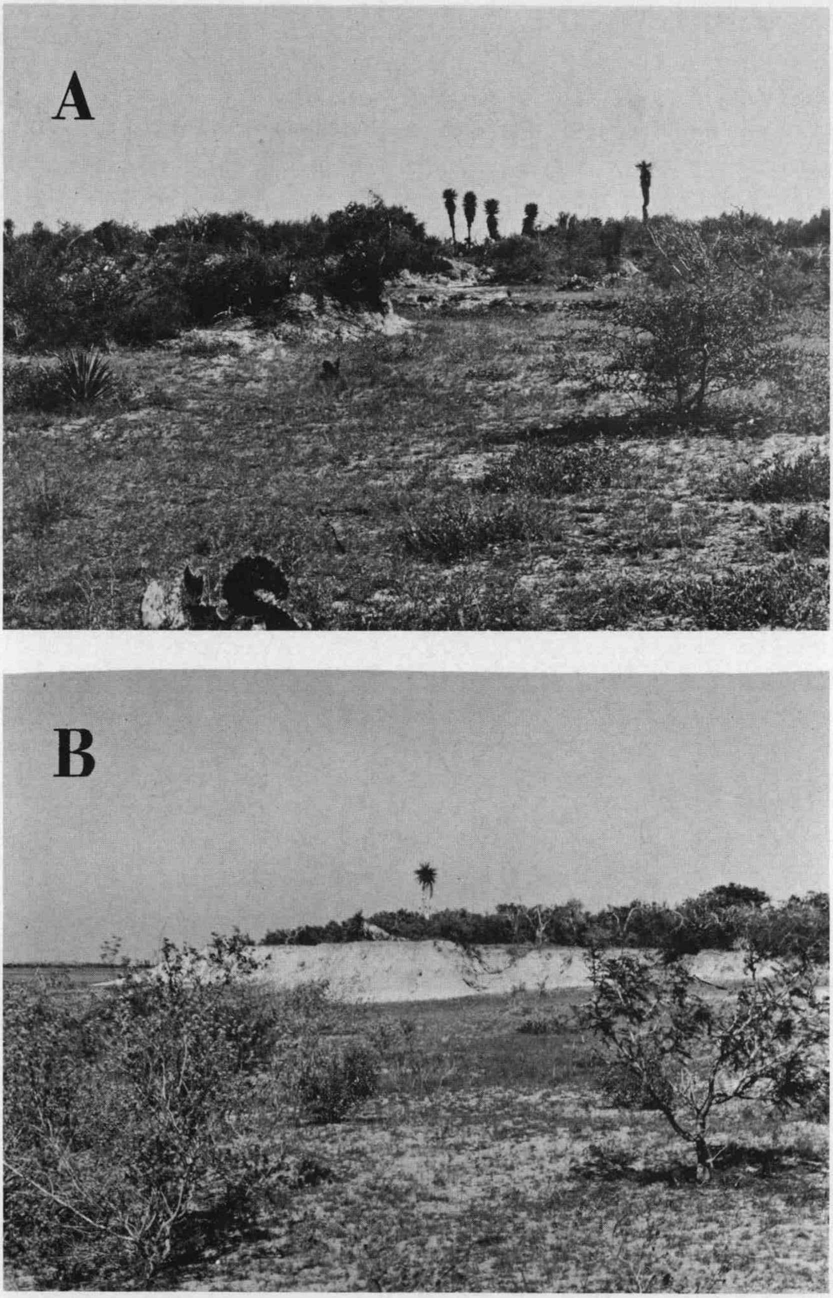


Figure 4. Loma Tio Alejos in southeastern Cameron County, Texas, looking toward the central higher area of the loma. A, shallow wash with outwash slope in foreground and thick brush in background. B, erosional bluff at top of the outwash slope; thick brush on top.

the western slope. At the periphery of the slope, and extending in a narrow band around almost the entire loma to the elevation of the surrounding playa flat is a zone composed almost exclusively of

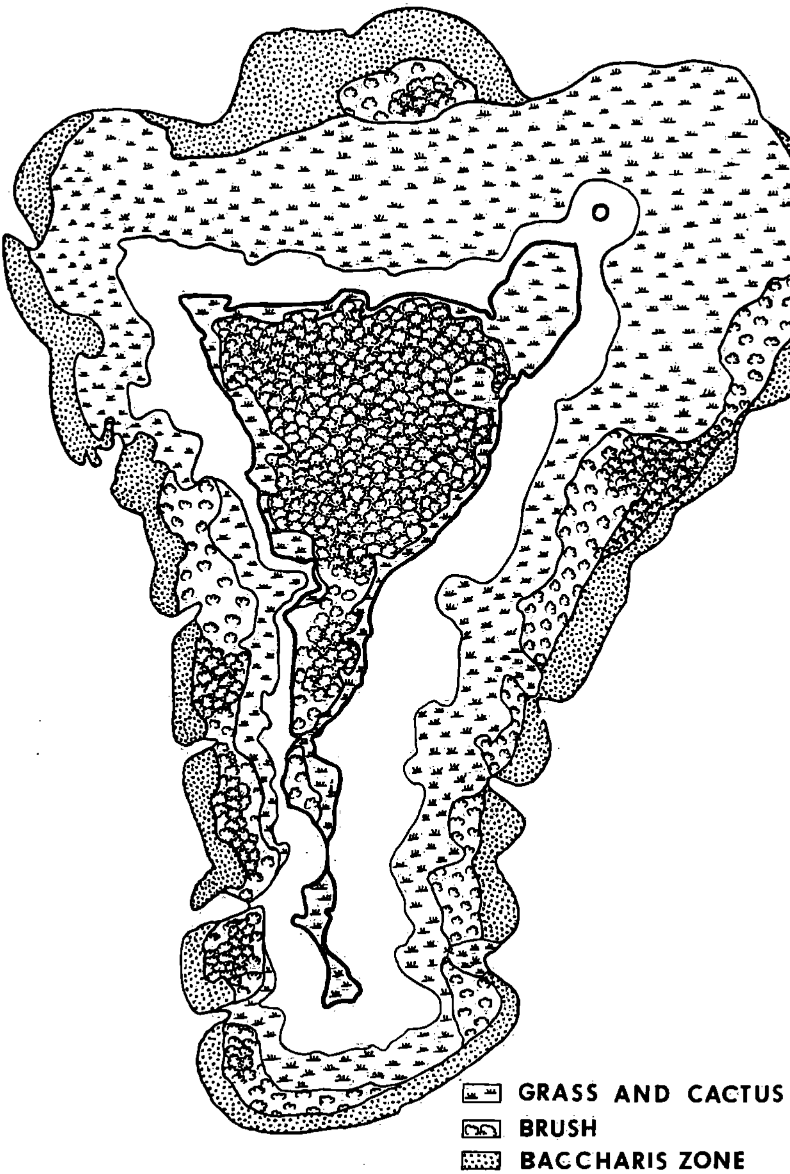


FIGURE 5. Distribution of major plant associations on the Loma Tio Alejos in southeastern Cameron County, Texas.

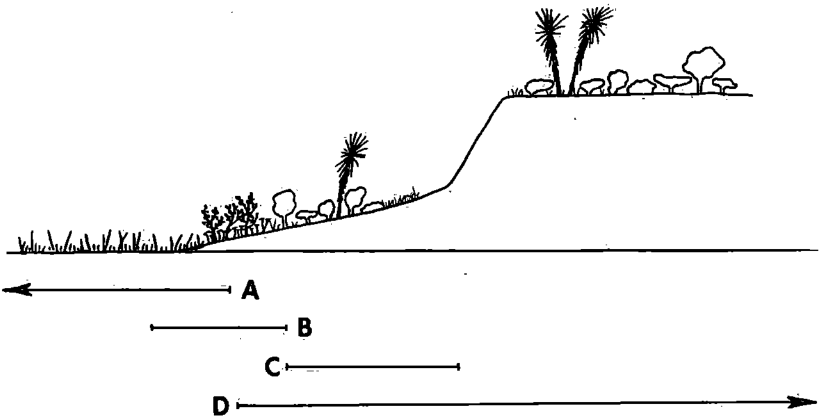


FIGURE 6. Distribution of dominant plants on the Loma Tio Alejos, southeastern Cameron County, Texas. Zone A (flats with characteristic halophilic plants): *Atriplex matamorensis, Batis maritima, Monanthochloa littoralis, Salicornia virginica, Suaeda linearis.* Zone B (transition Zone from outwash slope to flats): *Borrichia frutescens.* Zone C (outwash slope): *Aristida* sp., *Baccharis texana, Cenchris* sp., *Chloris verticillata, Citharexylum berlandieri, Hiliaria berlanderi, Karwinskia humboldtiana, Leucophyllum frutescens, Maytenus phyllanthoides, Plantago* sp. Zone D (includes plateau areas of loma and outwash slopes in early stages of erosion): *Acacia farnesiana, Berberis trifoliata, Bucheloe dactyloides, Castela texana, Celtis pallida, Condalia obovata, Condalia obtusifolia, Dalia argyraea, Lycium berlandieri, Opuntia leptocaulus, Opuntia lindheimeri, Pithecellobiam flexicaule, Prosopis glandulosa, Prosopis reptans, Xanthophyllum fagara, Yucca traculeana.*

*Baccharis texana* (Figs. 5, 6).

Most of the plants growing on the flats are halophillic. The dominant forms are soft grass *(Monothochoa littoralis),* salt wort *(Batis maritima),* and *Atriplex matamorensis.* All of these extend onto the lowermost portion of the outwash slope in favorable edaphic situations. The lowest parts of the flats are covered with extensive stands of *Spartina.* Many of the forbs and grasses die back during unfavorable periods of the year when precipitation is low or grazing pressure high. Only in spring when the cover of herbaceous vegetation is almost complete does the loma appear lush.

Essentially the same description applies to most of the lomas nearby, but the windward sides of those lomas surrounded by annually flooded, nonvegetated flats are presently accumulating wind-blown silt which is gradually suffocating the typical loma vegetation. The vegetation on these silt-covered areas is composed almost entirely of widely scattered pioneer species, of which *Croton argyran-*

FIGURE 7. Wind-blown silt and *Croton argyranthemus* on windward slope of the Loma de la Lena Seca, in southeastern Cameron County, Texas. Lomas are built from clayey silt deposited from flats such as those in the background.

*themus* is most common (Fig. 7). Few grasses grow in the drift areas.

On the younger, lower, but temporarily stabilized lomas, the grass cover is fairly extensive. These grasses are mainly 3-awn, panic, and sand bur. Shrubs and bushes, if present, are small and widely scattered. *Yucca* and *Opuntia* often comprise the tallest floral elements, though these too are widely scattered. These incipient lomas are often comprised of low, parrallel ridges and swales, the former having a higher surface sand content than the latter (Fig. 8-A). The swales are seasonally flooded with brackish water. The major vegetation in the swales are various species of brackish water sedges, grasses, and succulents.

## GEOMORPHOLOGY AND HISTORY

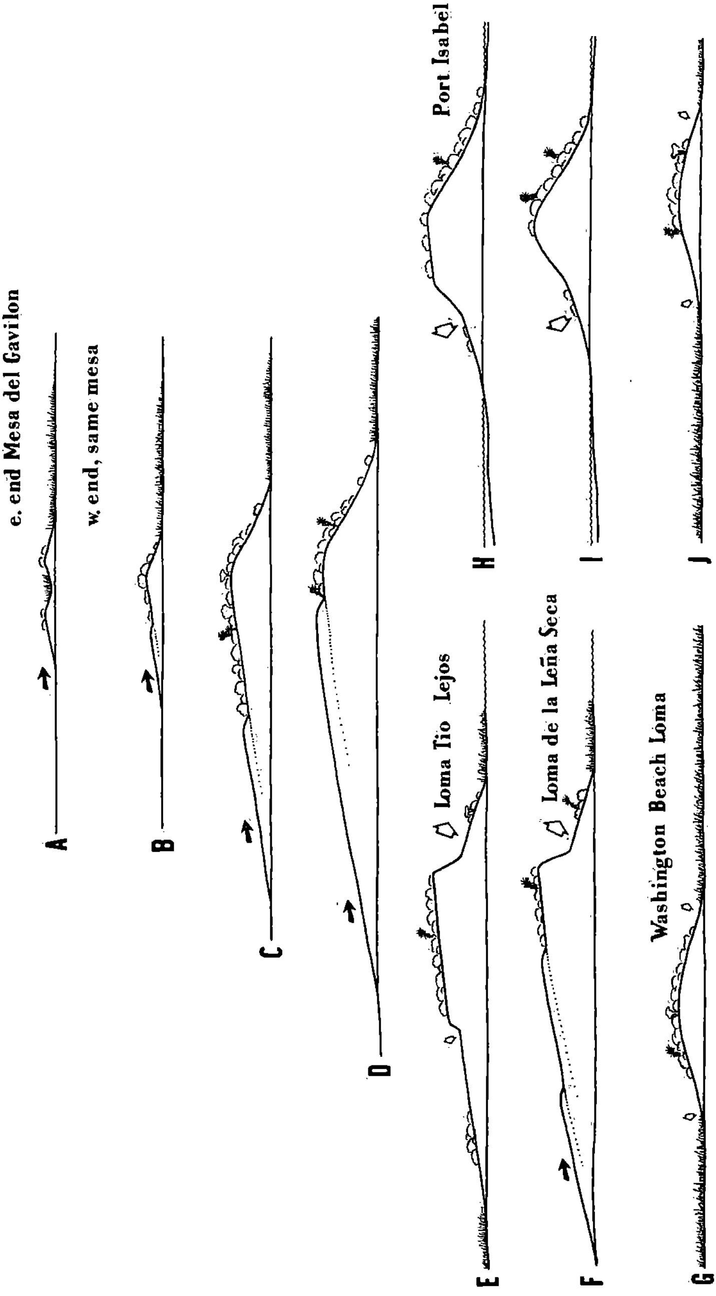
The area in which the study was conducted is a portion of the broadly embayed coastal plain of the west coast of the Gulf of Mexico. It lies within the meander belt of the Rio Grande and is a part of that river's deltaic plain.

The developmental processes along this part of the western Gulf are rather unusual in that alluvial deposition by the Rio Grande equalled the generally rising sea levels of the post-Wisconsin period. Consequently the entrenched river valley was not drowned inland from the continental hinge line, as were all the other large rivers along the Texas Gulf coast (Deussen, 1924; Price, 1954).

Two high-standing sea level substages are well recorded in coastal southeastern Texas. These are represented by the Late Pleistocene Beaumont plain and the Recent alluvial, deltaic, and interdeltaic depositional plains. The geological processes resulting in the formation of both these plains are very similar, differing only in their geologic age and stages of maturity (Weeks, 1945; Trowbridge, 1932).

The surface sediment of the study area is Recent Rio Grande alluvium overlying the Beaumont Clay. The postglacial north-south wandering of the easternmost end of the river, together with the annual flooding of its delta in April and May, particularly the Jackass Prairie, has been responsible for the deposition of this sediment. The recent construction of Falcon and Elephant Butte dams has largely prevented the massive annual flooding formerly characteristic of the area. Previously such flooding brought considerable silt into South Bay via several flood outlets north of the river. Historical records indicate that approximately 200 years ago an arm of the river emptied into South Bay throughout the year (Hedgepeth, 1953). In 1880 the mouth of the Rio Grande, then located near the eastern end of the Boca Chica road, moved south to its present position when hurricane waves built a sand bar over its former mouth. Tidal circulation into and out of South Bay was at that time still afforded by the old Boca Chica Pass, but when the Brownsville ship channel was dredged in 1938 the resulting spoil banks closed off much of this circulation. Reduced tidal scour at Boca Chica Pass and a later storm closed off the remaining circulation. As a result the mean water depth of South Bay was lowered 2½ feet, from 4 feet to 18 inches. Periodic redredging of the channel has tended to reduce the water level even more (Breuer, 1962). The result of all these factors is that more alluvial silt is now exposed in the playa flats of the southern part of South Bay than at any time within the historical record.

When not covered with either water or vegetation the exposed silt is easily removed by wind action. Strongest deflation of the flats occurs in summer, when flocculated saline clay accumulates on the lee shore of the playas and lagoons to build clay dunes (lomas) under the strong southeast winds characteristic of the area during


e. end Mesa del Gavilon
A
w. end, same mesa
B
C
D
Loma Tio Lejos
E
Loma de la Leña Seca
F
Washington Beach Loma
G
Port Isabel
H
I
J

this time of the year. Coffey (1909) and Huffman and Price (1949) describe similar eolian-deposited clay dunes near Corpus Christi, Texas, and have estimated that approximately one-fifth of the wind-blown clay excavated from the playa lagoon basins is caught on the dunes. The remainder passes inland as dust. Initially the silt apparently accumulates in low parallel ridges with swales between. The main axes of the ridges lie perpendicular to the prevailing wind direction. The eastern end of the Mesa del Gavilon is typical of this developmental stage (Fig. 8-A). These are the youngest habitable surfaces available to the tortoises of Jackass Prairie.

The ridges and their vegetation serve as windbreaks, trapping silt in the lee swales. Thus at a fairly early developmental stage the parallel ridge and swale structure is replaced with a low dune. Extensive dune growth depends on the continued availability of source materials from the nonvegetated playas windward of the developing dunes. If the flats or playas become vegetated, thus anchoring the silt, the dunes are temporarily stabilized regardless of their stage of development. Under these conditions northerly winds, tides and rain tend to erode the loma to the base level of the plain, eventually producing the low profiles seen in the lomas along the Washington Beach Road, east of Matamoras, Tamaulipas, Mexico (Fig. 8-G). These are the oldest habitable surfaces for tortoise populations on Jackass Prarie.

Subsequent loss of vegetation on the playas through massive silt deposition during river flooding results in the rejuvenation of dune formation, ending the predominantly erosional part of the cycle. The temporarily stabilized dune surface is then covered by another layer

FIGURE 8. Hypothetical development of the lomas in the study area, southeastern Cameron County, Texas. Lomas begin as a system of parallel ridges and swales (A), which act as a windbreak and accumulate wind-blown silt (closed arrows), rapidly assuming typical loma profile (B). If flats surrounding loma remain free of vegetation, loma continues to accumulate wind-blown silt (C and D, also see Fig. 7). If flats become vegetated after continued absence of salt water, lomas become temporarily stabilized, and erosion exceeds deposition (E, open arrows). Old lomas in advanced stage of erosion are shown in G and J. River or storm flooding may reduce vegetation on flats initiating new deposition cycle (F).

Lomas of study area on the south side of South Bay, (E, F) have gentle windward slope and steep lee slope from prevailing southeasterly wind and seasonal tidal erosion of north end. Lomas on north side of South Bay (H, I, J) near Port Isabel, have steep windward slopes cut by deep erosional gullies from year-round presence of wave and tidal action of lagoons on southeast side.

of wind-blown silt. Loma de la Lena Seca, just north of the Boca Chica highway approximately 4 miles from its terminus, is in this stage of development (Fig. 8-F). That dune coverage may be very rapid is shown by the fact that during a period of 4 years a silt blanket about 3 feet thick moved approximately 700 feet northwestward over one part of the Loma de la Lena Seca, or about 175 feet per year. This was established by comparing the extent of silt coverage in 1962 as shown by aerial photos of the loma taken with the limits of silt coverage established by direct observation in 1966.

The cyclic history of deposition on the lomas may be seen in the clearly marked bands exposed in roadcuts and eroded bluffs. The top of each band represents a stable, vegetated period. Such a history of erosional and depositional cycles has tended to keep the lomas in a dynamic equilibrium between pioneer successional plant stages and, as shown below, affects the behavior of tortoise populations inhabiting them.

Before dissection by erosion, the lomas are characterized by a gentle windward slope and a steep lee slope. In the southern portion of South Bay these lee slopes become more precipitous, with bluffs of 10 to 20 feet facing the bay. The formation of these bluffs is a result of several processes: (1) the prevailing southeasterly wind and its effect on dune cross-section; (2) differential rates of erosion on the windward and lee sides of the dunes resulting from differences in degree of slope; and (3) tidal and wave erosion on the north side of the dunes as a consequence of the northerly shift of the winds during the winter months and the resultant periodic flooding of the playas by tidal water (Fig. 8-E, F).

On the north side of South Bay the windward slopes of the lomas are steep and cut by erosional gullies. The rapid erosion on the windward instead of the lee side of these dunes undoubtedly results from wave action and tidal oscillation in the lagoons located southeast of these lomas (Fig. 8-H, I, J).

## POPULATION CHARACTERISTICS

### NESTS AND EGGS

During the study we were able to observe a number of nest features of *Gopherus berlandieri* not previously reported and to gather information from both captive and natural situations. In the only other report of nest building in *G. berlandieri* Sabbath (1960) reported that a female dug a hole 3 inches deep and 1¾ inches wide into which she layed 1 egg. In the present study we watched two captive tortoises dig nests, but none in the wild. The captive specimens, collected near Sinton, Texas, were kept in a large outdoor pen in Colorado.

Under the north side of a bush in the center of a circular enclosure 22 feet in diameter female A, carapace length 156 mm, built two shelters (called pallets, see section on shelters), to one or the other of which she retired each evening. At 07:45, 12 June 1961 she scraped the bare floor of the pallet occupied the previous night by using her epiplastral projection as a scoop. Starting at the pallet's shallow end she moved to the deep end pushing a small amount of dirt in front of her (Fig. 10-A). At the far end of the pallet, with the plastron still on the ground, she twisted her shell from side to side and moved laterally some of the dirt she had scraped up. She then used her front feet alternately to push the dirt either outside the pallet or onto her carapace. She then backed into her original starting position at the shallow end of the pallet and repeated the entire sequence. In 30 minutes she deepened the pallet's far end about ½ inch.

She now turned in the pallet to face the opposite direction and, with the rear portion of her shell in the lowest end, started to dig the nest with her rear limbs. Alternately she placed each hind leg medially under the plastron. As she drew the leg back to its normal position the outer edge of the plantar surface picked up a small amount of dirt and deposited it forward and laterally (Fig. 9). After

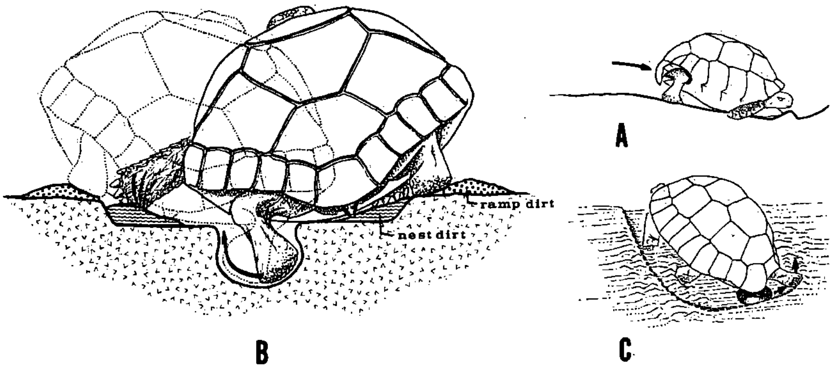


FIGURE 9. Major steps in nest construction by female *Gopherus berlandieri*. A. scraping out the nest ramp. B. nest excavation, showing major foot movements, body and limb positions, and ramp and nest spoil areas. C. nest excavation, showing hind limb movements in pushing dirt onto nest spoil areas.

repeating the scraping movements 2 to 4 times, she shifted the rear of her shell in the direction of the leg last used, thus bringing the opposite leg over the nest.

By 09:00 she was removing less dirt with each stroke. First the shape of the cavity itself made digging more difficult. The hole was now so deep that she had to draw each foot vertically to the surface, and she could bring up little soil on the foot in this manner (Fig. 9-B). Secondly the soil became increasingly hard with depth. This she partially overcame by urinating into the cavity. Bladder release seemed to be correlated with digging activity, for she dug more rapidly immediately after urinating, and the increased tempo removed considerably more earth. Also of help was the moist soil, which stuck better to the edge of her foot. As the soil again became dry the digging tempo decreased. Previous authors (Woodbury and Hardy, 1948; Carr, 1952; et al.) have attributed to urination during nest building solely a soil-loosening function. We noted that urination also helps by making the soil adhere better to the clublike feet.

The completed cavity was about 2¼ inches deep and 1¼ inches wide at the surface and had its greatest diameter 2 inches below the surface. One egg was deposited in the nest at 09:23.

Though this was the only egg this female laid in the summer of 1961, on 28 March 1962 two eggs were found in a cavity in the same pallet. It is not known if the same female dug this nest, as several others were kept in the same enclosure. The nest cavity measurements were: greatest depth 2½ inches; greatest width 2½ inches; diameter of opening 1½ inches.

At 08:00, 26 July 1961 female B (carapace length 186 mm) was noted sniffing the virtually bare patches of soil around the peripheral drip zone of a bush in an outdoor enclosure 12 feet in diameter in Boulder, Colorado. By 08:30 she had scraped one of these spots so that one end of the small cleared area was ½ inch lower than the other. Unfortunately a subadult *Gopherus polyphemus* then pushed her from the site and started to enlarge the deeper end, presumably to begin burrow construction. Although the *G polyphemus* was removed from the enclosure, the female *G berlandieri* did not resume nesting operations that day.

By 09:15 the next day she had built an identical clearing and slope immediately beside the pallet in which she normally rested. The deepest end was ¾ inches below the ground surface. Though no actual digging was noted until 12:15 that day, the nest cavity created in that time contained one malformed egg and some tortoise feces. Two days later this cavity was filled with earth, apparently by the same female.

On 17 June 1962 the same female scraped a second "nesting ramp" a few inches on the other side of its pallet. She began excavating at 08:10 and by 10:15 had deposited three eggs in a cavity 2 inches deep, 2¾ inches at its greatest diameter, and 1¾ inches in diameter at the surface. One of the eggs was at the very top of the nest cavity, the other two on the same plane at the bottom.

Captive tortoises often lay their eggs on the ground surface or on the floor of the cage, presumably because the proper nesting medium is lacking. Strecker (1929) reports finding 3 eggs under a tortoise in the field on ground so rocky that a nest could not have been dug. Grant (1960) reports finding 3 eggs on the surface on successive days after the same female had laid 3 eggs in a nest a few weeks previously. Once we found a single infertile egg on the ground surface in an opening in the brush cover on the Loma de la Estrella. Several nearby nest sites had already been destroyed by predators. The egg did not hatch when artificially incubated, nor did two other eggs found on the ground surface immediately adjacent to a pallet on the Loma Tio Alejos. We saw no cavity and the eggs seemed undisturbed by predators.

Several factors may influence the choice of nest site: (1) soil texture, (2) soil moisture, and (3) orientation with respect to the sun. Data gathered on these in the field permit the following generalizations:

1. The nest is normally constructed in soil relatively free of vegetation.
2. The nests are usually located under or near the drip zone of bushes.
3. No correlation is evident between nest site and the shade pattern of the bushes (Fig. 10).
4. A positive correlation exists between density of nest sites and density of tortoises, at least on the Loma Tio Alejos. Females use no specific nesting areas.
5. Nests usually occur in small clusters (Fig. 11), with considerable distance between clusters regardless of tortoise density. It is not known whether these clusters represent a series of nests dug by one, or by several females.
6. Nests are often found near, and even in the same spot under a particular bush in successive years. On the Loma de la Estrella we found four destroyed nests under a prickly ash in November 1963

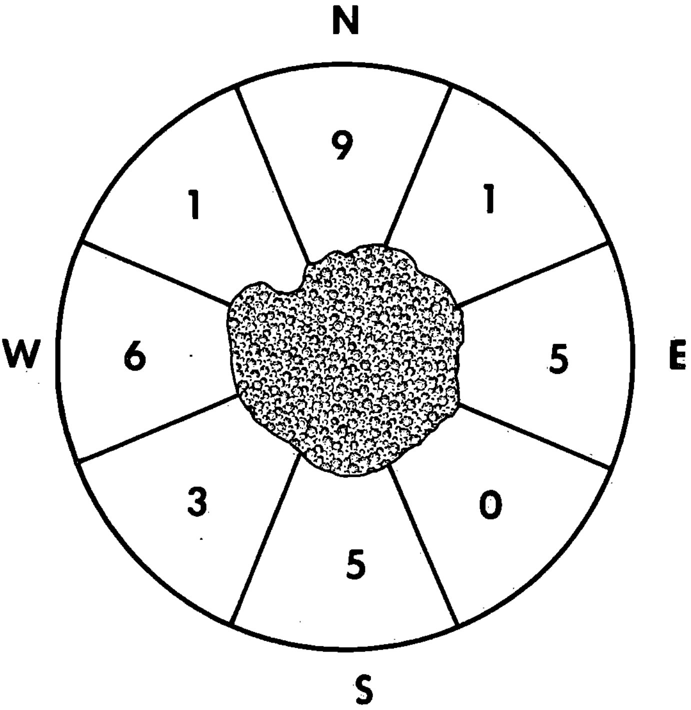


FIGURE 10. Thirty *Gopherus berlandieri* nest sites on the Loma Tio Alejos in southeastern Cameron County, Texas, and their location with respect to the closest shrub. Three nest sites were found near the shrub centers.

where we had found two in June 1962. It is not known if these nests were dug by the same female (Fig. 11).

Tracks in the soil near destroyed nests show that skunks and raccoons prey on tortoise eggs. *Neotoma micropus,* the southern plains woodrat, may also be an egg predator. Although, we have no direct evidence, the foreman of a nearby ranch told us of seeing them carry tortoise eggs in their mouths. That the woodrats do not use the eggs to enlarge their debris homes is clear, as we found no egg shells in these accumulations.

Predation data from a *Gopherus polyphemus* study (M.S.) in Lake County, Florida suggest that nests destroyed before hatching are usually lost within the first week following egg deposition. The same may be true in populations of *G. berlandieri* in Texas. Scents associated with nest building and egg laying are probably more important in leading predators to a nest than the scent of the eggs themselves.

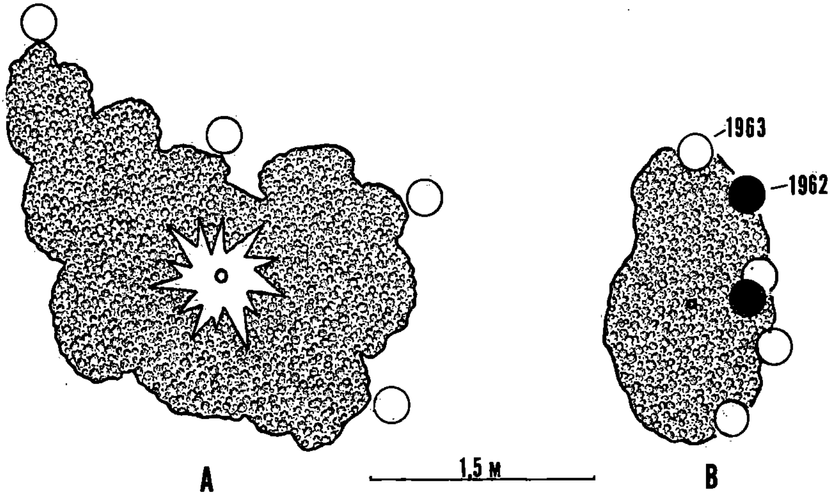


FIGURE 11. *Gopherus berlandieri* nest clusters on the Loma de la Estrella in southeastern Cameron County, Texas; A. around a shrub clump, 6 November, 1963; B. around a single *Berberus trifoliata* in 1962 and 1963. White circles = 1963 nests, dark circles = 1962 nests.

These associated scents probably disappear or become masked after a few days. We found one fully formed dead hatchling *G. berlandieri* in the field near a broken egg shell.

Very few nesting dates for *berlandieri* are available. Published records for egg laying are 22 June (Sabbath, 1960), and 8 July through 13 July (Grant, 1960). Additional information is now available. On 26 April 1966 we found several small holes on the Loma Tio Alejos that appeared to represent trial nest sites. Similar excavations were found there and on other lomas in August 1966. Freshly caught captive females laid from 8 June to 2 August. The earliest date we noted predator-destroyed nests in the field was 10 June, though some of these, judging by shell membranes that had already dried and fallen from the shell, were obviously several days old. Two eggs with shells were found in a female accidently killed in November 1965 during National Guard maneuvers in the study area. Shells found on the surface during the second week of November were obviously the result of predation on recently laid eggs. Freshly caught females sarificed in the laboratory contained shelled eggs as late as 16 September, and ovarian eggs larger than 10 mm in diameter as late as November; this shows nesting dates in southern Texas range from at least 8 June to 17 September.

Shelled eggs have been found in the oviducts as early as April, and eggs 10 mm or larger as early as March. Ovarian eggs were present in sacrificed females in March and April and again in September through November. Two mature females sacrificed in June and July had no ovarian eggs. The number of specimens sacrificed to determine egg content was small, and by itself inconclusive. These data, plus field observations, suggest two peaks in the production of both shelled eggs and egg laying, one in late June and July, the other in late August and September.

Whereas one to three eggs constitute the normal nest compliment range, individual females may lay several clutches each year. Grant (1960) reports that a captive female laid three eggs in a nest on 8 June, and later deposited single eggs on the surface on 19 June, 9 and 13 July. Under normal conditions this female probably would have built at least two nests. None of the eggs hatched. This information suggests that the previously mentioned clustering of egg sites may reflect multiple nesting of individual females. If so, some females must lay at least four clutches per year. It is not known whether each female lays every year, on in alternate years.

Data on the number of eggs per nest laid by individual females are available from three sources: (1) the number of eggs per nest estimated from the broken shells found at nest sites in the field; (2) the number laid in captivity; and (3) oviductal examination of females sacrificed in the laboratory.

We recorded in the field a total of 88 nests represented by egg shells only. Most had been excavated and destroyed by predators, but some apparently had hatched. We assumed that egg remains consisting of two or three large fragments more or less in place in the nest site represented a successful hatch. Similar egg fragmentation has been recorded after hatching in captivity. Scattered egg fragments and such signs of predator intervention as digging were considered to represent unsuccessful nesting (Fig. 12). The number of eggs could reasonably be established in 60 of these nests: 38 nests contained one egg each, 19 contained two eggs and 3 contained three eggs. Of 13 clutches laid in captivity 8 had one egg each, 4 had two eggs, and 1 had three eggs. The combined wild and captive records are: 46 clutches of one egg, 23 clutches of two eggs, and 4 of three eggs. Data on numbers of eggs per clutch laid by other species of the genus are much the same. Miller (1932) suggests that the nests of *G. agassizi* contain only one egg, but Grant (1936) and others show the normal compliment varies from one to

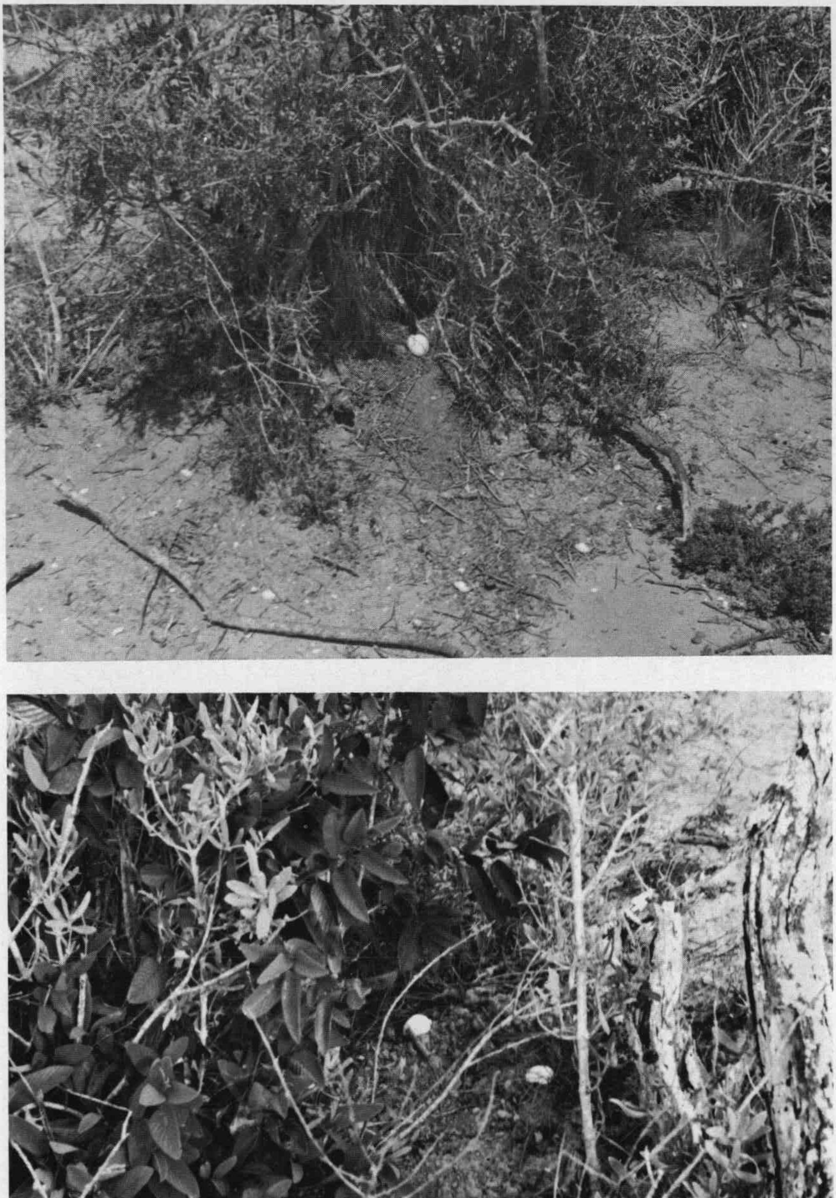


FIGURE 12. Nests of *Gopherus berlandieri* in southwestern Cameron County, Texas, destroyed by predators.

six. In *G. polyphemus* the number of eggs per nest varies from two (W. A. field notes) to seven (Carr, 1952).

Measurements in mm of nine shelled eggs of *G. berlandieri* are: 48.3 × 32.4; 43.6 × 35.0; 53.7 × 32.6; 52.2 × 32.2; 46.5 × 35.6; 47.4 × 34.3; 48.2 × 35.6; 49.0 × 33.8 and 47.4 × 34.8 (width/length ratio 0.61 to 0.80, mean 0.71). Grant's (1960) measurements of 6 eggs from Hebbronville, Texas are similar (width/length ratio 0.66 to 0.82, mean 0.73). Sabbath (1960) described a single egg of similar size (46 × 32). The eggs of *G. agassizi* and *G. polyphemus* are generally more spherical (Grant, 1936; Carr, 1952).

## HATCHLINGS

Almost no information is available on hatchlings of *G. berlandieri*. Agassiz (1857) figures a specimen (pl. III), but does not describe it in the text, other than mentioning its dimensions (41 × 41 mm). Woodbury (1952) figures and briefly describes a presumed hybrid of *berlandieri* × *agassizi* that resulted from a mating described earlier by Householder (1950). Hatchlings of *agassizi* have been described by several authors (Woodbury, 1931; Miller, 1932; Grant, 1936; Woodbury and Hardy, 1948; *et al.*). Those of *G. polyphemus* have been described by Allen and Neill (1953), Neill and Allen (1957), and Arata (1958). The hatchlings of *G. flavomarginatus* are unknown. A hatchling *berlandieri* (UF 23943, 40 × 41 mm) found dead on the surface at Mesa del Gavilon (Fig. 13), but associated with a broken shell, was obviously very close to hatching or had just hatched. Its description follows:

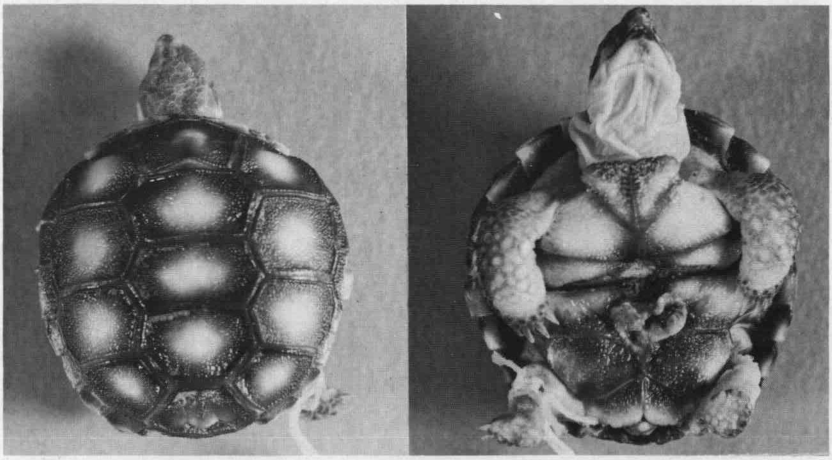


FIGURE 13. Hatchling *Gopherus berlandieri* (UF 23943), Mesa del Gavilon, 14 miles E. Brownsville, Cameron Co., Texas.

In general, the color pattern is similar to that of hatchlings of *G. polyphemus* and *agassizi*, but darker (Agassiz' figured specimen is even darker). Pigmented areas of the shell are dark brown, unpigmented areas creamy white. The unpigmented areas on the anterior marginals are restricted to the posterior edge of each scute, to the free edges on the lateral and posterior marginals, and to the center of each costal and vertebral scute (smaller area than in any specimens of *polyphemus* and most specimens of *agassizi* seen). The plastral pigment is restricted to the scute seam areas except on the femoral scutes, where pigment covers all but the free lateral edges. The head has a yellowish stripe running from below the anterior corner of the eye to the angle of the jaw. The tympanic region is unpigmented. There is a faint yellowish temporal patch, also a small unpigmented spot around the egg tooth and both nostrils. The throat and chin are creamy white with a dark spot at the mandibular symphysis. The horny mandibles are dark, and the remainder of the head is dark brown. The scales at the base of both fore and hind feet are black. The dark scales on the hind feet continue back around the lateral side of the heel and up the hind leg for a short distance, with the remainder of the hind leg a creamy white, except for the yellowish thigh scales. The dorsal tail surface is grayish. The outer brachial scales are black, while those of the middle anterior portion of the front limb have light yellowish centers; those of the inner edge are completely cream white. The scales of the posterior brachial surface are dark on the dorsal half of the brachium and lighter below, with the skin color of the upper and lower arm sharply differentiated just above the elbow.

The proportions and shape of the hatchling *berlandieri* differ somewhat from those of *agassizi* and *polyphemus*, but resemble *agassizi* more than they do *polyphemus* (Table 1).

Table 1. HATCHLING CHARACTERS OF *Gopherus*

| Characters | *berlandieri* | *agassizi* | *polyphemus* |
|---|---|---|---|
| Gular scute | Greatly projected | Intermediate | Not projected |
| Laminal spurs | Absent | Absent | Present |
| Marginal denticulations | Absent | Absent | Present |
| Head width | Narrow | Narrow | Broad |
| Posterior plastral lobe | Short, wide | Longer | Longer |
| Pigmentation | Extensive | Intermediate to little[1] | Proportionately very little[2] |

[1] See Miller (1932) for variation data.

[2] Slightly darker on west coast of Florida peninsula and in Appalachicola River valley. See Arata (1958) for variation data.

The umbilical scar is just disappearing in a 48 mm specimen (UF 16565, Zavala County, Texas), collected approximately 6 months after the latest probable hatching date.

## SIZE

*G. berlandieri* is the smallest of the four extant species of *Gopherus*. Beyond this, little is known of the species' size characteristics. Our size data reveal differences in tortoise populations of reasonably closely situated, but individually isolated lomas.

Secondary sex characteristics are clearly evident only in *berlandieri* larger than 105 mm. Males attain a greater size than females, as clearly illustrated by the Loma Tio Alejos population where males averaged approximately 8½% larger than females (Table 2). Essentially the same relationship occurs in populations on the Port Isabel Loma (males 8% larger) and the Mesa del Gavilon (males 9% larger) though the sample sizes for each of these populations are much smaller. The Loma Tio Alejos individuals are similar in size (Fig. 14) to more inland populations near Laredo, Alice, San Diego, and Sinton, Texas. Individuals from the Port Isabel Loma and Mesa del Gavilon are larger than the Loma Tio Alejos specimens. The largest specimen of this species reported so far is 214 mm in shell length (Carr, 1952). As discussed later, many of the Port Isabel males are younger than smaller male specimens on the Loma Tio Alejos; the size differences are apparently due to differential growth rates on the different lomas. The three largest specimens we have measured, all males, are UF 18101, near Odem, Texas, 219 mm, and

Table 2. SOME POPULATION PARAMETERS OF *Gopherus berlandieri* POPULATIONS IN SOUTHEAST TEXAS

| Parameter | Location | | |
|---|---|---|---|
| | Loma Tio Alejos | Port Isabel Loma | Mesa del Gavilon |
| Per cent adult males | 27.7 | 46.6 | 20.0 |
| Per cent adult females | 57.6 | 53.4 | 40.0 |
| Per cent nonadults | 14.7 | — | 40.0 |
| Average shell length of females | 140.8 mm<br>n = 36 | 148.4 mm<br>n = 8 | 166.7 mm<br>n = 10 |
| Average shell length of males | 167.0 mm<br>n = 75 | 195.5 mm<br>n = 7 | 183.7 mm<br>n = 5 |

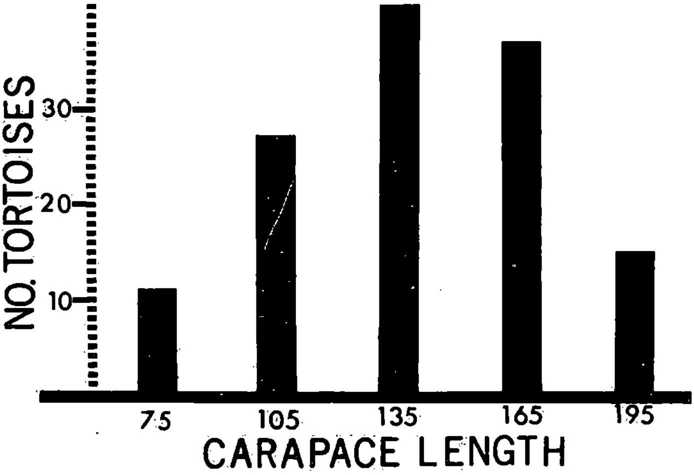


FIGURE 14. Size distribution of *Gopherus berlandieri*, Loma Tio Alejos, southeastern Cameron County, Texas. N = 130, class interval ± 15 mm. Carapace length in mm.

UF 19562 and UF 23036, both from near Brownsville, Texas 218.2 mm and 217 mm. The largest ones that Carr (1952) reports have all come from southeastern Texas.

## GROWTH

Determination of actual growth rate in nature demands data of a type and quantity unavailable to us in our studies, but the rate of growth can be estimated from the several recognizable size classes within the smaller individuals of the population. The carapace length at hatching is approximately 50 mm. No growth is evident beyond the central areolae of each scute. The next size class ranges from 70 to 81 mm, and these specimens show only one noticeable growth ring beyond the areola, suggesting they are one year of age. The mean size increase in the first year after hatching is 50.3%. This increase is smaller than that calculated (68.1%) for the first year of growth in *Terrapene ornata* (Legler, 1960). Identification of larger size classes and correlative examination of major growth rings in these classes suggest that sexual maturity is attained at from 3 to 5 years of age (Fig. 15), or from 105 to 128 mm. None of the tortoises larger than this can be placed in distinctive size groups, although many larger specimens show major annual growth rings. This suggests that the growth rate slows markedly at about 6 years of age (shell length about 130 mm) and thereafter remains more or less

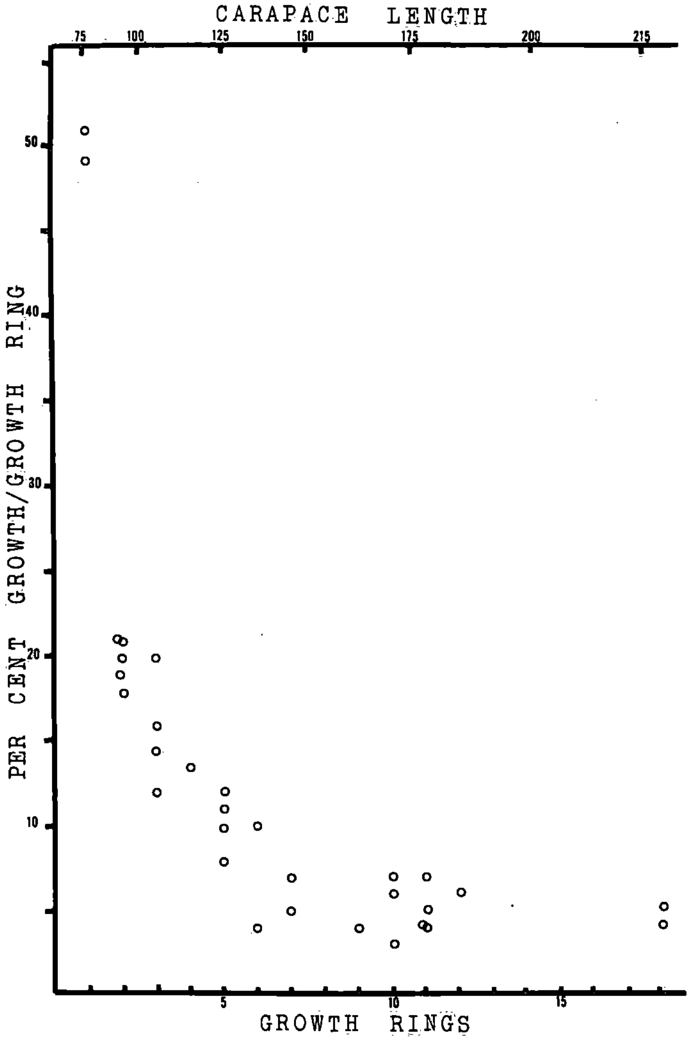


FIGURE 15. Average annual percentage growth rate for *G. berlandieri* on the Loma Tio Alejos in southeastern Cameron County, Texas.

constant at approximately 5% per year (Fig. 15). The maximum number of major rings counted in any specimen was 18 (201 mm), but the number can not be counted accurately in most specimens larger than 180 mm.

The average absolute growth for males is 7.9 mm per year and 12.5 mm per two years, for females 11.1 mm per year and 18.9 mm for two years, suggesting that females may grow slightly faster than males.

## COLOR

As in many other organisms color and size are related in *berlandieri*, and a general relationship between size and age may also be assumed. To obtain data on the relationship between color, size, and age, the frequency of tortoises in each of three color groups (black and yellow, brown, and yellow and brown) was plotted against size. Black and yellow tortoises are more common from hatching through the 140-160 mm size range. The 160-180 mm size range shows a pronounced increase in the number of brown individuals. The brown and yellow individuals represent a transitional color phase between a black and yellow pattern and a solid brown color, and occur most frequently in the 140-160 mm size class. This was one of several reasons influencing our division of tortoises into two size groups ($<150$ and $>150$) in the movement section. Thus we regard young tortoises as including both black and yellow and brown and yellow individuals. Sexually mature individuals are found in all three color classes. That black and yellow individuals may be sexually mature is attested by the fact that some of them breed and lay eggs. Old tortoises are always a light brown or "horn" color.

## DENSITY AND DISTRIBUTION

Only for the Loma Tio Alejos are the data sufficient to provide more than a rough estimate of population density. Data for analysis are based on 193 tortoises known to live on the loma. As the area of the entire loma is approximately 85,500 square meters, the minimum overall density is 430 square meters per tortoise. As we found a few unmarked tortoises on every visit, the actual density is probably slightly greater than this. Nonetheless we believe that the total counted is close to the actual total for the loma. We assume that the unmarked tortoises are not immigrants from other lomas primarily because of the distances such moves would involve and the lack of shelter from the sun in the intervening flats. Reasons for considering the populations of each loma as more or less isolated are discussed more fully below.

Even casual observation makes it obvious that the tortoises are not evenly distributed on the loma. Therefore we determined tortoise density in each of the characteristic plant associations of the loma. Only the first sighting of each tortoise was used in the analysis, regardless of season, year, or activity of the individuals. Thus each tortoise was for purposes of density estimates counted only once, regardless of where it was subsequently recaptured on the loma. Of the four major plant associations on the loma, tortoises are most dense in the brushy area (Table 3), although considerable variation occurs within each of the associations. For example, tortoise density in the brush on the outwash slope (1 tortoise per 64 M$^2$) is much greater than in the brush on top of the loma (1 tortoise per 1429 M$^2$). We have no evidence of seasonal variation in these densities.

Table 3. DENSITIES OF *Gopherus berlandieri* IN THE THREE MAJOR PLANT ASSOCIES ON THE LOMA TIO ALEJOS

| Plant associes | Area (M$^2$) | Number | Density |
|---|---|---|---|
| Brush | 9,750 | 119 | 1:82 M$^2$ |
| Baccharis Zone | 7,500 | 25 | 1:300 M$^2$ |
| Grass and Cactus | 48,000 | 39 | 1:1,231 M$^2$ |
| Clay Zone | 15,750 | 10 | 1:1,575 M$^2$ |
| Totals | 85,000[1] | 193 | 1:430 M$^2$ |

[1] Includes approximately 4,500 M$^2$ of brush too thick to be investigated.

Though definitive data are lacking, tortoise densities for corresponding plant associations on adjacent lomas are probably comparable. However densities on the open eastern end of the Mesa del Gavilon are lower than on any comparable area on the Loma Tio Alejos. Careful search revealed only three tortoises on its small, sparsely vegetated area. On the Port Isabel Loma the difference between the high tortoise density on the middle of the lee slope and the very low density at its base is marked, though the plant association is continuous. On the Loma de la Lena Seca tortoises wander far over the windblown silt in search of food. Population density on the silted area is very low, though in the adjacent brushy areas it is probably comparable to that of the brush on the Loma Tio Alejos. In the open drier brush complex of Falcon Dam State Park, Starr County, Texas, we estimated the density to be about 1 tortoise per 42,000 square meters.

## MOVEMENT

From November 1963 through April, 1966, 159 tortoises were marked on the Loma Tio Alejos by drilling 1/8 inch holes in the peripheral bones according to a 6-digit code. Data recorded upon capture and recapture included time of day, location, activity in which the tortoise was engaged, color of cloacal discharge, sex, and carapace length. After coding and recording data at the place of capture the tortoises were released. Thus the captured and recaptured data represent known geographic point occurrences of each tortoise. In order to indicate the place of capture more accurately, the loma was marked off in a grid of 50-meter squares. The location of each tortoise was first determined as to square, and then within each square by obvious landmarks. The original location of the tortoise and those of subsequent recapture were transferred to a large-scale map of the loma, based on topographic maps (Palmito Hill Quadrangle, U. S. Geol. Surv.), available high altitude aerial photos (S. E. Cameron County, map 6, U. S. Dept. Agric.), and low-level aerial photos taken by the senior author. Movement between captures was measured on the map as the straight-line distance from the original point of capture. This method of determining movement was selected because we felt it would be a better test of the reality of the activity range of the type described in *Chrysemys scripta* (Cagle, 1944), *Terrapene* (Stickle, 1950; Legler, 1960), and *Gopherus agassizi* (Woodbury and Hardy, 1948).

The recapture data were analyzed in three ways: accumulative movement between 1, 2, and 3 years; movement per trip; and movement per day. Within each category the data were analyzed according to sex and size. Data on daily movements were obtained by using a spool and thread trailer similar to that described by Stickle (1950) (Fig. 16), and by following tortoise tracks in the sand or silt. The analysis of accumulative annual movement was designed arbitrarily to compare the movement of two size classes of tortoises; those greater and those less than 150 mm in carapace length.

Table 4 shows that tortoises 150 mm or shorter move farther than larger ones. No correlation is evident between sex and distance

Table 4. CUMULATIVE AVERAGE YEARLY MOVEMENT (IN METERS) OF *Gopherus berlandieri* ON THE LOMA TIO ALEJOS

| Shell length | Sex | 1 year | 2 years | 3 years |
|---|---|---|---|---|
| 150 mm > | Males | 98.6 (12)[1] | 153.0 (8) | 130.0 (5) |
| | Females | 94.1 (13) | 92.4 (11) | 164.1 (6) |
| | Means | 96.6 (25) | 118.0 (19) | 149.0 (11) |
| 150 mm < | Males | 30.0 (2) | 149.1 (3) | 178.0 (1) |
| | Females | 93.7 (19) | 162.0 (11) | 302.0 (6) |
| | Means | 87.5 (21) | 159.5 (14) | 284.0 (7) |

[1] Figures in parentheses are recaptures per visit.

FIGURE 16. Daily movement data were obtained by means of a thread trail, released by the mechanism pictured.

traveled. All tortoises tend to move away from the original place of capture.

Records of daily movements (Fig. 17, Table 5) indicate a tendency to maintain a temporary activity range. Of eight turtles tracked by a thread trail, three (field numbers 321, 104, 203) returned within 2 days to the pallet in which they were originally captured, and one (field number 21) returned to the same bush in which it was originally captured but to a different pallet. Only one (field number 331) showed no definite tendency to maintain a restricted activity range during the observation period. Those tortoises with activity range (approximately = home range) indices approaching or exceeding unity are regarded as having a weak tendency to maintain an activity range. The average maximum distance traveled per day was 20.6 meters and the average distance of the night pallet from the original was 8.3 meters. The patterns in figure 17 reinforce the thesis that the tortoises, while nomadic, maintain restricted activity ranges for

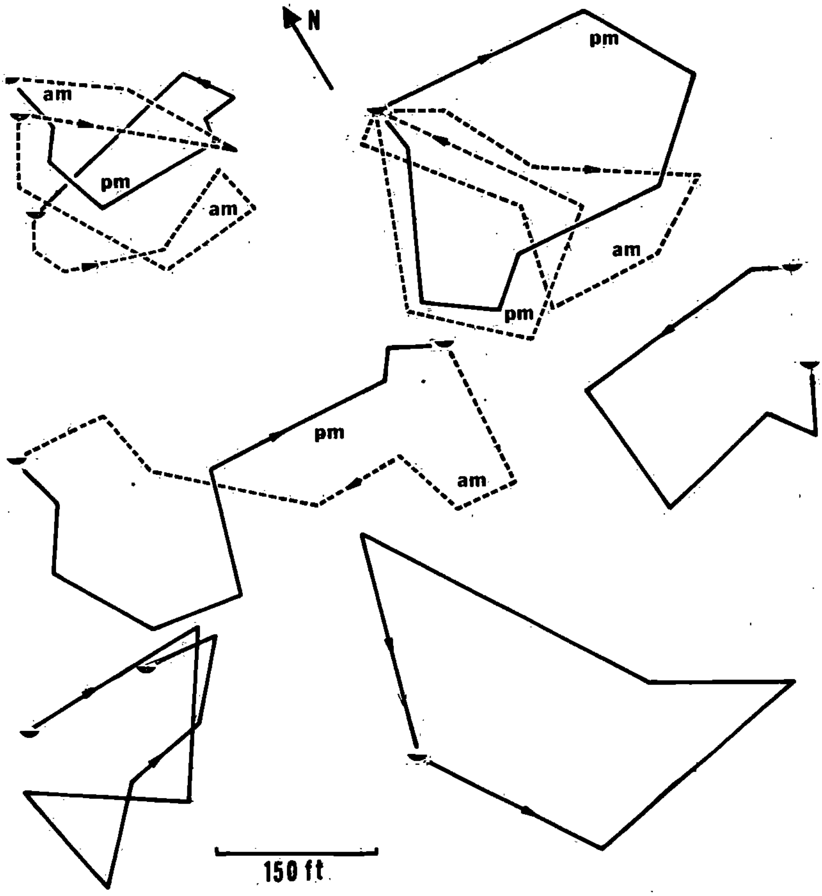


FIGURE 17. Typical daily movements of six *Gopherus berlandieri*, Loma Tio Alejos. Solid and dotted lines represent successive days. The small hemispheres represent pallets used. Data gathered by thread trails. See Table 5.

short periods of time. The average observed distance tortoises traveled during an average visit (1 week, Table 6) is intermediate between daily and yearly average distances. These tortoises are therefore primarily nomadic, and maintain restricted activity ranges for only a few days between successive greater or lesser secondary movements.

In addition to tracing movements on the Loma Tio Alejos, we also followed tortoise movements on several other lomas in various stages of plant succession and geological development. Our findings suggest that daily movement at least is influenced by the successional

Table 5. DAILY MOVEMENT OF *Gopherus berlandieri* ON THE LOMA TIO ALEJOS

| Tortoise number | Shell length (in mm) | Sex | Max straight line distance (in meters)[1] | Pallet distance (in meters)[2] | Home range index[3] |
|---|---|---|---|---|---|
| 321 | – | ♀ | 22.0 | 21.3 | 0.97 |
| | | | 21.3 | 0.0 | 0.00 |
| 104 | 113 | ? | 15.5 | 0.0 | 0.00 |
| | | | 15.8 | 0.0 | 0.00 |
| 21 | 120 | ♀ | 10.7 | 4.6 | 0.37 |
| | | | 10.7 | 1.5 | 0.14 |
| 331 | 152 | – | 42.6 | 42.6 | 1.00 |
| | | | 52.5 | 95.0 | 1.81 |
| 51 | 159 | ♀ | 5.2 | 4.8 | 0.92 |
| 303 | 159 | – | 16.4 | 7.9 | 0.48 |
| 304 | 168 | – | 12.2 | 7.0 | 0.57 |
| 203 | 171 | ♀ | 18.9 | 0.0 | 0.00 |

[1] Distance moved from original pallets.
[2] Distance between new and original pallets.
[3] Maximum straight line distance/pallet distance.

stage and geological age of the loma. For example, the tortoises on the Loma de la Lena Seca, on which wind-blown silt is currently being deposited, move greater distances per day than tortoises on the other lomas studied. The tracks four tortoises made in a single day across the wind-blown silt measured 46.0, 161.0, 142.0, and 480.0 meters. The mean distance of daily movement for three accumulative years on the Loma Tio Alejos is 267.0 meters. The reason for these movement differences between tortoises of the two lomas obviously is related to food availability. The accumulating silt has suffocated much of the vegetation and hence food, on the Loma de la Lena Seca (Fig. 7).

Table 6. AVERAGE DISTANCE MOVED BY *Gopherus berlandieri* ON THE LOMA TIO ALEJOS DURING EACH OBSERVATION PERIOD

| Shell length (mm) | 1963 | 1964 | 1965 | 1966 | 1966a | Means |
|---|---|---|---|---|---|---|
| 150> | 42.8(10)[1] | 178.0(4) | 86.0(2) | 151.0(3) | 32.7(3) | 86.2(22) |
| 150< | 36.8(10) | 41.7(8) | 55.5(5) | 32.5(1) | 60.5(4) | 55.7(28) |
| Means | 39.8(20) | 104.9(12) | 79.8(7) | 91.8(4) | 46.6(7) | |

[1] Figures in parentheses are recaptures per visit.

### ACTIVITY PERIODS

Daily activity periods recorded for April, June, and July show that the tortoises have two principal activity periods, one in the morning, and one in the afternoon. Table 7 shows the tendency for activity periods to become better defined in June and July. By July (and August, according to unrecorded data that admittedly are open to subjective bias) most tortoises are active in the afternoon after 15:00 or 16:00. We found no differences in activity period with respect to size or sex.

Subjective observations for November (1963) suggest that the daily activity pattern resembles that available for April (1966) in that we made more midday and fewer late afternoon and morning observations.

Table 7. DAILY ACTIVITY, LOMA TIO ALEJOS

| Time of day | 25-29 April 1966 | 10-13 June 1966 | 13-17 July 1964 | 9-22 July 1965 | Totals |
|---|---|---|---|---|---|
| 05:00-07:00 | 0 | 1 | 3 | 0 | 4 |
| 07:01-09:00 | 2 | 7 | 15 | 15 | 39 |
| 09:01-11:00 | 15 | 1 | 0 | 4 | 20 |
| 11:01-13:00 | 6 | 0 | 0 | 0 | 6 |
| 13:01-15:00 | 0 | 0 | 0 | 0 | 0 |
| 15:01-17:00 | 11 | 0 | 3 | 17 | 31 |
| 17:01-19:00 | 0 | 1 | 28 | 14 | 43 |
| 19:01-21:00 | 0 | 0 | 0 | 1 | 1 |
| Totals | 34 | 10 | 49 | 51 | 144 |

### ORIENTATION

In June 1966 we performed several preliminary field experiments to test the ability of *G. berlandieri* to recognize a home range and orient within it. We released tortoises at various distances and directions from the pallets in which we found them and traced their movements for 36 hours by means of a thread (Fig. 16). We made 5 releases on the Loma Tio Alejos and 11 on the adjacent flats away from typical tortoise habitat (Tables 8 and 9; Figs. 18 and 19). Releases on the loma reinforce the daily movement data that suggest a temporary activity range (Fig. 17). The cues the tortoise uses to recognize its activity range remain unknown, but are presumed to be visual or olfactory landmarks. That local features may aid a tortoise to recognize its activity range is suggested by the movements of tortoises released on the featureless flats. These showed no consistent ability to reach the loma from two release points 50 and 125

Table 8. Homing Ability of *Gopherus berlandieri* released on lomas

| Distance removed from pallet (in meters) | Compass direction from pallet | Distance from pallet at end of test (in meters) |
|---|---|---|
| 42.5 | E | 20.7 |
| 31.0 | S | 31.0 |
| 49.6 | WSW | 27.9 |
| 100.1 | SSE | 37.2 |
| 77.6 | E | 0.0 |

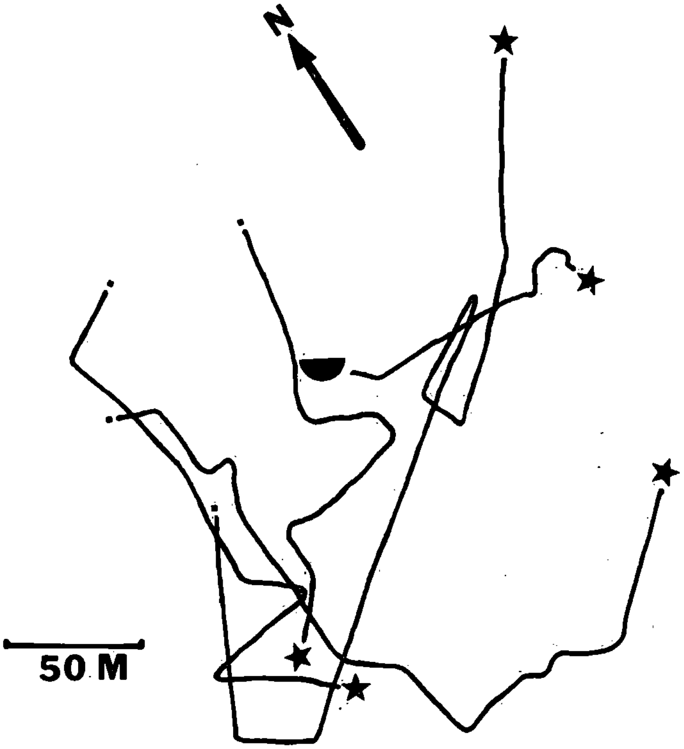


Figure 18. Thread trails of five different *Gopherus berlandieri* released (star) at varying distances and directions from the pallet (hemisphere) in which they were found on Loma Tio Alejos, southeastern Cameron County, Texas. The dots show where the tortoises stopped for the evening. Tortoises show a general tendency to move in the direction of their pallets. See Table 8.

meters distant from the loma edge (Fig. 19).

The vegetative differences between the lomas and the flats may

Table 9. HOMING ABILITY OF *Gopherus berlandieri* RELEASED ON FLATS

| Distance released from loma (in meters) | Final distance from loma (in meters) | Final heading (+ = toward loma, – = away from loma) |
|---|---|---|
| 108.5 | 155.0 | – |
| 108.5 | 0.0 | + |
| 93.0 | 0.0 | + |
| 87.0 | 87.0 | – |
| 108.5 | 54.4 | – |
| 108.5 | 0.0 | + |
| 108.5 | 136.4 | – |
| 105.0 | 0.0 | + |
| 54.5 | 82.2 | – |
| 54.5 | 54.4 | – |
| 49.6 | 65.2 | – |

be partly responsible for the disorientation shown by tortoises released on the flats. We found no evidence that tortoises regularly cross the flats from one loma to another, or that they even make short

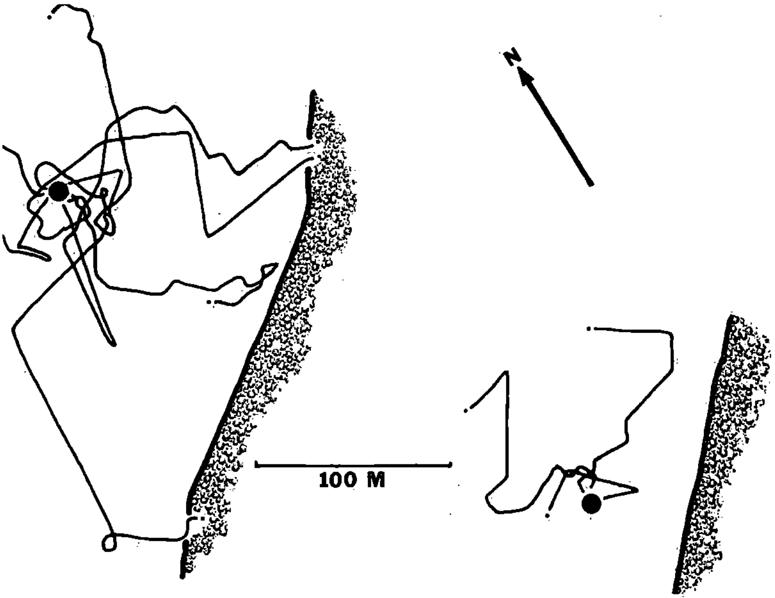


FIGURE 19. Thread trails of 10 *Gopherus berlandieri* released on the flats west of the Loma Tio Alejos, southeastern Cameron County, Texas. The tortoises had no consistent ability to reach the loma (brush symbols to right) when released approximately 50 and 100 meters from the loma edge. Dots indicate the final resting place of the tortoises. See Table 9.

forays onto the flats from a "home" loma. On the contrary we found that tortoises avoid wandering onto the flats at all. On the Lomas de la Lena Seca and de las Vacas tracks are easily followed over wind-blown silt. We tracked many tortoises from the central vegetated parts of the loma to the loma-flat border and then back onto the loma. Several tracks paralleled the loma edge – one for several hundred meters. Only one tortoise wandered out onto the adjacent flat, and then only for a distance of about 10 meters before turning back.

Wandering over the flats from one loma to another would usually be fatal to a tortoise because of the lack of shade, and could only be done in cool, cloudy weather. Obviously such trips have been made in the past, as tortoises occur on most of the lomas. We do not believe, however, that these populations were seeded primarily by any tendency of the tortoise to wander onto and over the flats. The seasonal flooding of Jackass Prairie by the Rio Grande before the Falcon and Elephant Butte dams were built may have been an important means of transporting tortoises from one loma to another. That flooding can displace tortoises without fatal results is shown by populations of *G. agassizi* near Tucson, Arizona, whose members often survive being swept considerable distance by seasonal flooding of the arroyos along which they live.

The geological history of the Jackass Prairie shows that in advanced stages of loma erosion the raised level of the intervening flats is modified through deposition. The raised level of the flats encourages the growth of larger, shade-producing plants and reduces the density of halophytic vegetation. These changes would improve the chances of successful dispersal across the flats. Thus more frequent interloma exchange is expected over the older, more vegetated and consequently more stable flats, than over the lower, seasonally innudated, geologically younger, and vegetatively barren flats presently being deflated by wind erosion.

## SHELTER

Over most of its range *G. berlandieri* spends almost all of its resting periods in a form or pallet it makes by scraping away the ground litter and soil over an area slightly larger than itself, normally at the base of a bush, under a cactus clump, or a tuft of grass. In the following account the anterior end of the pallet is the end that projects into the ground and against which the tortoise rests the front of its shell. This is usually little more than a sloping ramp the tortoise makes by using the epiplastral projection, the front limbs, and the lateral edges of the shell. Within the activity range of almost every individual are several active, cleaned-out pallets, as well as a number of old, trash-filled ones. Recapture and thread trail records show that the individual tortoise uses several of the pallets within its daily activity range. The directness with which tortoises walk to particular bushes under which active pallets are located within their activity ranges suggests that they know the exact location of at least some of these pallets.

Anteriorly the pallet is usually deep enough to conceal the dorsal front edge of the tortoise's shell (Fig. 20). Before using an unoccupied pallet, the tortoise often pushes out the accumulated soil and vegetable matter. The continued use and clearing of specific pallets tends to deepen them, and some much-used pallets in the Brownsville area become deep and overhanging enough to cover the entire tortoise. The deepest pallet we found on the clay lomas was approximately 13 inches long and 4 inches deep at its anterior end. Such deepening may be fairly rapid. One pallet with a 1-inch overhang in 1962 was extended by an unknown number of tortoises to an 8-inch overhang by 1963.

The literature on the use of burrows as opposed to pallets by *G. berlandieri* is not conclusive. Carr (1952) states that though *G. berlandieri* burrows have been reported, he found none in the clay soils of Tamaulipas, Mexico. True (1882) doubted that the species ever used burrows. Grant (1960) reported on correspondence received from V. M. Lehman, Wildlife Manager of the King Ranch, Kleberg County, Texas, who stated that though tortoises are often found in burrows in the local sandy soils, he doubted that the tortoises excavated them; rather, he believed that they simply utilized existing burrows of large mammals. At Falcon Dam we found the tortoises using both the holes made by coyotes digging for rodents and the dens of armadillos. Our evidence suggests that while tortoises do use mammal burrows, they can and do excavate their own. We found one tortoise burrow that was approximately 4 feet long and 1 foot deep in a caliche soil 5 miles west of San Diego, Duval County, Texas, 18 June 1965; fresh tracks from this burrow led us to the animal. In sandy soil 3 miles north of Laredo, Webb County, Texas on 16 June 1966 we found two holes with the typical hemispheric cross section of *Gopherus* diggings; one was 2′ 10″ and the other 4′ 3″ long, both were about 12 inches below the surface at their deep ends. Though the Laredo burrows were empty, their

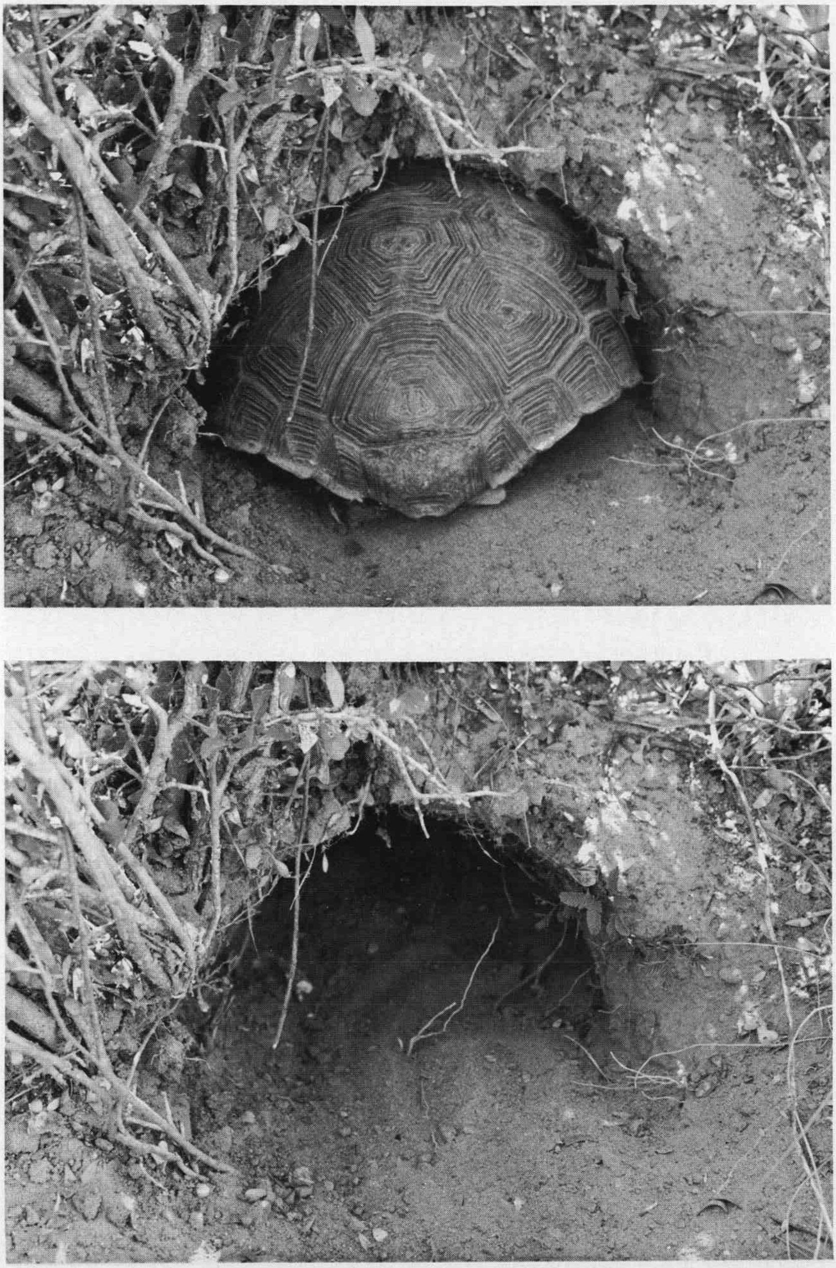


FIGURE 20. Top. *Gopherus berlandieri* in a typical pallet, Mesa del Gavilon southeastern Cameron County, Texas. Bottom. Same pallet empty.

entrances suggested recent use. In both areas we found normal pallets. That these burrows were used solely as winter shelters is doubtful. Possibly such burrows are used more commonly in the northern than in the southern portions of the species' range, but Guy Austin, Curator of Reptiles, San Antonio Zoo, told us he knew of no tortoises in that area that dug or retreated to burrows at any time of the year. He reports that in winter they simply "shuffle themselves down into the soil until the shell is about an inch or two below the surface." Grant (1960) describes similar winter activity in this species near Hebbronville, Jim Hogg County, Texas. Immediately after a "norther" in November, 1961, we found a tortoise on the surface near Sinton, Texas that had just extricated itself from such a depression.

In August 1966 we found two tortoises in burrows they themselves had obviously dug in sandy soil on the eastern part of the Mesa del Gavilon, several miles east of the Loma Tio Alejos. One, an adult female, was in a burrow 33 inches long and about 12 inches deep at its end below a small clump of *Opuntia* (Fig. 21). That this burrow had been used for a long time was suggested by trails leading away from it through the surrounding three-awn grass that were practically identical to trails leading from the mouths of established burrows of *G. polyphemus*. The second specimen, a juvenile, was in a small burrow 7½ inches long, excavated under a board lying on the ground surface.

Near Brownsville we found pallets and short burrows in the accumulated rotten cactus pads of old and active *Neotoma* nests. One short burrow extended into the almost disintegrated base of a rotten mesquite stump. Carr (1952) collected specimens under stumps and rubble heaps in Tamaulipas, Mexico.

These records suggest that *G. berlandieri* is highly opportunistic regarding use of shelter. In sandy soils, where holes are easily excavated, and where the lack of shade in summer or the cold of winter encourage such activity, some individuals may dig a burrow. In other regions, such as the low sandy lomas near the Boca Chica beach, individuals possibly spend much of their lives in such burrows. In still other areas, such as San Diego and Laredo, burrows may be used intermittently or only in the winter. In all parts of their range the tortoises modify the burrows of other animals and use any other available shelter such as old, or even active, pack rat houses. It is perhaps significant that deep burrows are not excavated into poorly drained soils, such as clay. Because the major soil type within its

FIGURE 21. Entrance of *Gopherus berlandieri* burrow, approximately 1 meter long, in sandy soil, Mesa del Gavilon, southeastern Cameron County, Texas.

range is a type of feldspathic clay, the species usually constructs a pallet rather than a burrow for shelter. In some regions these pallets may be deepened in the winter to cover most, or all of the shell. A similar behavioral variation in the excavation and use of shelters is known in both *G. agassizi* and *G. polyphemus* (Auffenberg, in press). The factors governing the type and use of shelters by populations of all three species are (1) the extent of seasonal extremes in surface temperatures, and (2) substrate composition.

On 11 November 1963, we measured 92 active pallets and short burrows on the clay soils of the Loma Tio Alejos in two dimensions: 1) the extent of the overhang at the deepest end and 2) either the length of the tortoises found in the pallet, or if empty, the width of the pallet. The width measurements were converted to approximate tortoise shell lengths. That the width of a tortoise's burrow or pallet is approximately equal to the tortoise's carapace length is the basis of the conversion. The data for pallet depth, as measured by the extent of the upper overhanging lip, shows that pallet overhang is negatively correlated with tortoise length. In the Loma Tio Alejos, juvenile tortoises tend to dig a proportionately deeper pallet than larger animals (Fig. 22). Tortoises less than 100 mm long characteristically dig a pallet longer than their own shell length, with one exception — a juvenile found wedged under the fallen trunk of a honey mesquite. Of 10 juvenile tortoises in the size range 60-100 mm found in pallets, all but one had pushed dirt behind them plugging the opening to their short burrow. This dirt plug is probably important in both water balance and predation. In the most arid parts

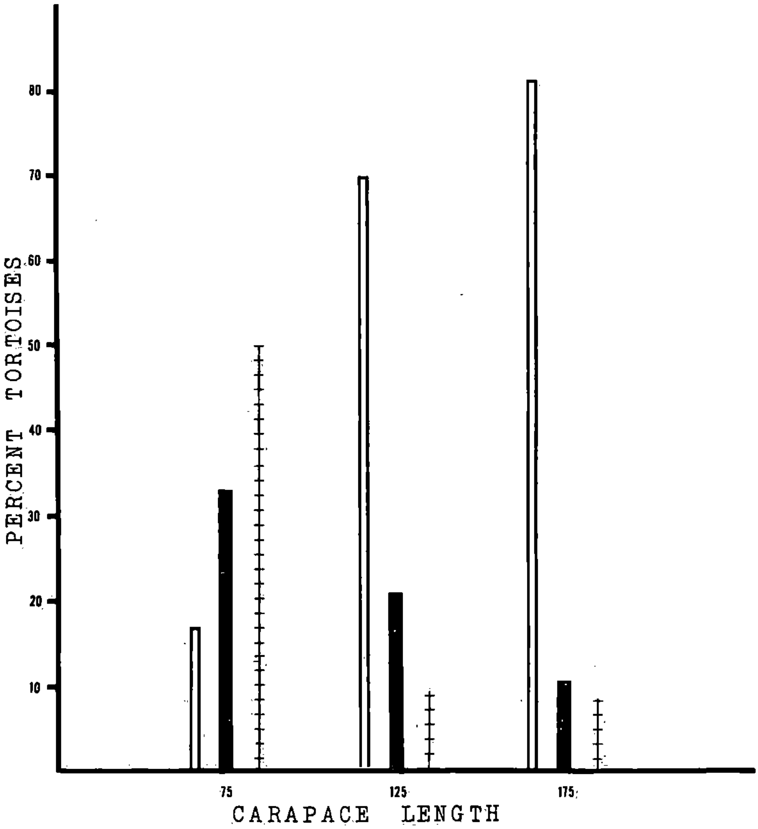


FIGURE 22. Carapace length and relative pallet overhang of *G. berlandieri* on the Loma Tio Alejos in Cameron County, Texas. Pallet overhang/carapace length ratios as follows: 0-1.0, white column; 1.1-2.0 solid column; 2.1 and over, crossed column.

of *agassizi's* range adult individuals also make similar plugged burrows in the exceedingly hot and dry summer months.

Pallets are usually in a slight depression, against the side of a small surface irregularity, or against the base of a tree, shrub, or a cactus pad. We have seen tortoises enlarging both active and nonactive pallets made by smaller individuals. One tortoise dug a pallet in a small depression one of us made a day earlier when searching for very small tortoises. Another was seen enlarging the deepest part of a cow hoof print for its pallet.

Some evidence indicates that pallet use is seasonal. Pallets in the thick brushlands on the Loma Tio Alejos definitely are used throughout the year, but in summer (June, 1966) proportionately more tortoises are found in pallets in the thick brush than in open areas. In winter (November, 1963) a greater proportion of tortoises are found in pallets in open brush or grassy areas (November: 16 in pallets located in thick brush, 24 in open brush or grass; June: 19 in pallets in thick brush, 10 in pallets in open brush or grass).

## FOOD AND FEEDING

Data on feeding and food preferences in *G. berlandieri* are available from both field and laboratory studies. Table 10 summarizes identified plant remains from droppings collected in the field during August 1966, most of it composed of several types of grasses. In the wild we have seen tortoises eat the feces of other tortoises and of rabbits. In captivity we have also observed them eating the grass-filled droppings of their own and other tortoise species. In addition to the plant remains listed in Table 10, one crayfish claw, several broken land snail shells, and a few fragments of beetle elytra have been identified in the feces.

Country people living in the range of *G. berlandieri* are well aware that one of the commonest plants these tortoises eat is the cactus, *Opuntia*, a food preference also reported in the literature (Grant, 1960; Mittleman and Brown, 1947; *et al.*). Of the two species of *Opuntia* found in the immediate study area, *O. lindheimeri* is eaten more often. The tortoises feed on its pads, fruits, and flowers. Pads knocked to the ground by grazing cattle are often eaten before they become desiccated. The tortoises also eat the upright, growing pads along their lower edges when within reach. We have seen individuals with their noses nearly covered with the small areolar spines of this cactus, and some on their tongues as well. We found several individuals with large spines working their way out of the masseter

Table 10. PLANTS IDENTIFIED IN DROPPINGS OF *Gopherus berlandieri* POPULATION, CAMERON COUNTY, TEXAS
+, abundant; L, leaves (some stems); F, fruits.

| | Loma de la Lena Seca | Mexican Loma[1] | Loma Tio Alejos | Port Isabel Loma | W. end, Mesa de Gavilon |
|---|---|---|---|---|---|
| *Opuntia lindheimeri* | | L+, F+ | L+, F+ | L, F | L+, F+ |
| *Opuntia leptocaulus* | | | F | | |
| Grasses (*Bucheloe, Chloris,* and *Aristida*) | L, F+ | L+, F+ | L+, F+ | L+, F+ | L+, F+ |
| *Cenchris* | | | F | F | F |
| *Plantago* | | | F | | |
| *Monothochloa* | | | L | | |
| *Prosopis reptans* | | | L | | |
| *Citharexylum* | | | | | L, F |
| *Xanthophyllum* | | | L+ | L+ | L+, F+ |
| *Condalia obovata* | | | L | L+ | L |
| *Celtis pallida* | | | F | | F |
| *Berberis* | | | L | | |
| *Lycium* | | | L | | L |
| *Maytenus* | | | L | | |
| *Viola* sp. | | | F | | |
| *Aster* sp. | | | F | | |

[1] Sample considerably less than from remaining areas.

muscles on one or both sides of the head. One specimen that died in captivity had its small intestine completely blocked by a small cactus pad that was still spiney.

The fruits of both *Opuntia lindheimeri* and *O. leptocaulus* are eaten either red (ripe) or green. Ripe fruits not eaten by other animals eventually fall to the ground, and these the tortoises seem particularly partial to. The fruits and pads are an important source of water as well as nutrition. *Opuntia lindheimeri* flowers occur in two color varieties on the Loma Tio Alejos, yellow and reddish orange; we have seen tortoises eating both.

While *Opuntia* is eaten commonly, its use is somewhat seasonal in the study area. When the lomas are lush with the spring rains in April, grass is the most common food. *Opuntia lindheimeri* is eaten increasingly in the summer when the grass starts to wither. Though the pads are available throughout the entire year, cactus flowers appear only from June through August. The fruit of the previous year begins to ripen in June and by July becomes a major part of the tortoise diet. At approximately the same time the "urine" changes color from a murky brownish-red or clear yellow to clear red, reflecting the dietary change to ripe *Opuntia lindheimeri* fruits. The fruits of *Opuntia leptocaulus* normally ripen in October and November, and they are eaten mainly during this period.

Other food habits and/or preferences seen in *G. berlandieri* include biting the bleached bones of cows and rabbits on several occasions. Carr (1952) reports similar behavior in *G. polyphemus* in Florida. Herbivore nutritionists associate this with diets low in phosphate rather than in calcium as commonly believed. Captive *G. berlandieri* accept a great variety of fruits and vegetables if not too tart or bitter. Lettuce supplemented with bone meal and occasional fruits seems an excellent and easily obtained diet for captive specimens.

## COLOR PREFERENCES

Grant (1960) notes that *G. berlandieri* shows a decided preference for red-colored food, and he relates this preference to the ripe fruit color of *Opuntia lindheimeri*. The senior author initiated in 1964 a broader study of color preferences in various populations of all species of *Gopherus*, the results of which are to be published later. The color preferences shown by *G. berlandieri* are included here for the sake of completeness.

Two groups of six adult males and six adult females each were tested for color preferences in two periods: 1 May to 28 June, 1964, and 2 August to 5 October, 1965. The testing device was a series of three metal tabs each colored differently with electrical current-conducting Dykem Metal Dyes, (Dykem red, blue, and light green), and connected to a Grayson-Stadler "Drinkometer" vacuum switch requiring 0.6 millivolt for circuit closure. Each vacuum switch was connected to an electric digital counter. The switches were fastened inside a container on the floor of the pen housing the tortoises. A wire guard over the metal tabs prevented accidental contact. A tortoise could make contact only by deliberately placing its head through the spaces in the wire guard and touching the tab. The linear sequence of the three colored tabs was changed every 5 days during each of the two experimental periods of 30 days each. Table 11 shows the results obtained during the two test periods.

These tests reveal that (1) red and green are bitten more often than blue, supporting Grant's contention, and (2) the 12 tortoises caught in the spring and tested in May and June bit the green tabs proportionately more than the 12 specimens captured in the summer and tested in August and September. The shift to red in the labora-

Table 11. Seasonal Color Preference of *Gopherus berlandieri*

| Test period | Red | Blue | Green | Totals |
|---|---|---|---|---|
| May and June | 96[1] | 13 | 121 | 230 |
| August and October | 192 | 48 | 22 | 262 |
| Totals | 288 | 61 | 143 | 492 |

[1] Number bites per color tab.

tory experiments is in accord with field observations on food color changes. During the summer ripe red cactus fruits are substituted for the green grass of the spring. The relatively large number of responses to blue during the August-October tests is perhaps explained by the presence at this time of the year of ripe bluish-black fruits such as those of *Citharexylem,* which the tortoises are known to eat.

## PREDATION

Little is known about post-hatchling predation on this species. Predation pressure on adults is probably rather low. One adult female found dead on the Loma de la Estrella in November 1963 obviously had been dragged out of its pallet, killed, and eaten the preceding night. The only carnivores in the area large enough to accomplish this feat are coyotes and bobcats. Though the inhabitants of Port Isabel claim one jaguar lives in the general area, it is said to stay usually near the coast north of the ship channel. Pieces of tortoise shell are often seen in the rubble houses of the southern plains wood rat, *Neotoma micropes.* That the wood rats kill the adults is doubtful, but they may be the most important single predator on hatchlings in view of their apparent predation on eggs. On the other hand, juveniles, and particularly hatchlings, are probably often eaten by most carnivorous animals large enough to break away the shell. This category includes foxes, coyotes, skunks, bobcats, and raccoons. The remains of one tortoise no more than 1 year old found on the surface of the Loma Tio Alejos (UF 21914) lacked the rear third of the shell and body; the predator remains unknown. In Florida adult indigo snakes *(Drymarchon corais)* are known to feed on hatchling *G. polyphemus* (pers. comm., Robert Mount). This snake is reasonably common on the lomas of the study area and may represent still another source of hatchling predation. The same species of snake eats hatchling red-legged tortoises *(Geochelone carbonaria)* in Panama.

Human activity is without question the most important single factor affecting the distribution and population density of *G. berlandieri*. Many of man's effects are direct, such as the removal and/or killing of individual tortoises or populations, but probably even more important are his indirect effects by habitat destruction or modification. In southern Texas the shift from cattle raising to field crops, particularly cotton, destroyed thousands of acres of the region's unique brushlands. Mexico has a long history of severe overgrazing, a practice that continues to destroy additional thousands of acres of tortoise habitat.

The next most important factor is undoubtedly the automobile. Untold hundreds of tortoises are killed on the highways of Texas and Mexico every year, many deliberately. Perhaps the most distressing activity is the collection and sale of hundreds of specimens for the pet trade. Though better adapted to captivity than other species of *Gopherus*, individual *G. berlandieri* seldom live long outside their normal range, and most individuals slowly starve on a diet of insufficient variety to supply their mineral and vitamin requirements. Many ranchers deliberately kill the tortoises because of a mistaken notion that they break or eat quail eggs. Fortunately the State of Texas has recently passed legislation protecting *G. berlandieri.*

On the positive side are several human activities favoring the tortoises, the most important of which is probably the effect of managed grazing in tortoise habitats, as discussed in preceding sections. Even more dramatic, but longer range effects can be seen in brush control areas where successional development of the mesquite-chaparral community is maintained as a vegetatively ecotonal area. This practice, while initially killing many tortoises, increases grass production, and under current brush control practices the scattered brush cover the tortoises need reappears very quickly. If, in addition, the area is grazed by cattle, it is maintained in a dynamic equilibrium in which tortoises maintain their maximum densities over long periods of time. Slight overgrazing under such conditions encourages the growth of the prickly pear, *Opuntia*, one of the staple foods of *G. berlandieri* when grasses become dry in the summer.

## DISCUSSION

Perhaps the most important contribution of our studies on *Gopherus berlandieri* is the behavioral variability demonstrated between the populations in the study area. Such variability is surprising in view of the relatively short distances between the lomas to which the tortoise populations are restricted. At the root of the behavioral differences lie differences in the geological and vegetational histories of each of these lomas. The major differences in interpopulational behavior, such as shelter construction, activity range, and food preference are all closely interrelated.

The tortoises of the genus *Gopherus* are characteristically found in the arid and semiarid portions of southern United States and Mexico. Here where water, food, and shade all are often scarce, tortoises are able to survive more by their ability to modify regulatory behavioral patterns than on their physiological limitations. Not the least important of their homeostatic activities is the ability of individuals of all four species to escape critical temperatures and humidities by excavating a simple shelter of some type.

Of the nine living genera of tortoises only *Gopherus* includes species that habitually dig long, deep burrows in the ground, (Auffenberg, in press). The front limbs of the extant species are specialized for this purpose to varying degrees. The most specialized limb is found in *G. polyphemus* in which the feet and forelimbs are remarkably flattened and spade-like, with stout, relatively immovable digits provided with robust, flattened claws. Whereas the wrist of most other tortoises can be moved to a limited degree, that of *G. polyphemus* is made largely immovable by strong, sheet-like ligaments that bind the bones into a more or less solid unit (Auffenberg, 1966). Thus the limb is functionally a small spade, providing the tortoise with an effective soil-moving device. Of the living species of *Gopherus* the limbs of *berlandieri* are the least specialized for digging.

*G. polyphemus* is an essentially non-nomadic species that usually lives on sandy soil in ecotonal situations where it usually digs a long, unbranching burrow (Fig. 23). Though these tortoises live in what appears to be a dry habitat, the end of the burrow is generally moist. This moisture is apparently one of the most important of the factors determining the depth of excavation (Hansen, 1963; *et al*). Although evidence shows that new burrows are sometimes excavated, each individual normally uses a single burrow throughout its life with the burrow diameter and length increasing with the animal's growth. The tortoises leave their burrows almost every day to graze on the vegetation found within several hundred feet of the burrows.

This behavioral pattern is not characteristic of all the populations

FIGURE 23. Entrance of typical burrow of *Gopherus polyphemus*, Astor Park, Lake County, Florida.

throughout the species' range. For example, in at least one area in Levy County on the west coast of Florida some individuals do not dig burrows, but shelter themselves in a shallow form or pallet under a tuft of grass or bush. The region these tortoises inhabit is warm throughout most of the year. The substratum is moist; the land surface is just a few feet above sea level, and only a few inches of soil overlie the limestone bedrock. Still another atypical situation is represented by some individuals on Marco Island, Collier County, Florida where a single individual may use both burrows and pallets, the pallets apparently on warm, moist nights and the burrows the rest of the year.

In the relictual grasslands of the interior drained Bolson de Mapimi at the junction of the Mexican states of Durango, Chihuahua, and Coahuila, is a second species of burrow-digging tortoise, *G. flavomarginatus*. Recently discovered and poorly known, this species is similar to *G. polyphemus* in both morphology and habits (Legler, 1960; Legler and Webb, 1961; Auffenberg, 1966). During the Pleistocene its range extended approximately 300 miles south of its present southern limits in Mexico, and north at least to southern New Mexico. Thus its present distribution is only a small remnant of a range that previously embraced almost all the Mexican plateau. The burrows of this species extend into the hard, baked soil of the playa basins to depths of at least 8 feet. Like *G. polyphemus*, the Mexican bolson tortoise grazes along feeding paths leading from the burrow mouth through the surrounding grasses.

The third species is the desert tortoise, *G. agassizi,* of southwestern United States and northwestern Mexico, which has the largest range of all the *Gopherus* species. The great variety of soil types and temperatures included in its range are reflected in the ecologicial behavior of the constituent tortoise populations.

Individuals living at the southern edge of the species' range in Sonora, Mexico, are completely nomadic throughout most of the year. The activity range of individual tortoises is apparently very large, though mostly restricted to the dry arroyos that dissect the region. The shelter most commonly used is a shallow hollow dug into the base of the arroyo wall (Fig. 24). Several individuals use the hollow during a season. Each occupant enlarges it slightly by scraping at the walls for a few moments before settling for the night.

The pattern of shelter construction and use by individuals of the same species in the rocky arroyos of Pima County, Arizona, is similar, except that the lower winter temperatures demand more protection. Hibernation takes place in specific shelters to which individual tortoises often return year after year. These hibernacula are always located well above the arroyo floor and are usually simply an enlargement of a ground squirrel burrow. Normally the excavated enlargement extends only deep enough so that the rear portion of the tortoise's shell is flush with the arroyo wall. This is apparently enough to remove the tortoise from the cold night winds and yet exposes a part of its shell to the afternoon sun.

Because these hibernation sites are usually on south-facing arroyo slopes, and because the tortoises enlarge the burrows of local mammals able to excavate their own galleries only in certain kinds of bank strata, the number of available over-wintering sites is limited. This factor frequently leads to winter aggregations of tortoises in Arizona, where four or five individuals are "parked" in adjacent "garages" during the colder months (Fig. 24).

Still another behavioral pattern has been described for populations at the extreme northern edge of this species' range in southeastern Utah (Woodbury and Hardy, 1948). Here the tortoises have two distinct activity ranges — a large warm weather range on the desert flats where they excavate short burrows in the shallow soil, and a

FIGURE 24. Upper. Pallet scraped into arroyo wall by *Gopherus agassizi* near Aduana, Sonora, Mexico. Lower. Individual *G. agassizi* hibernacula, near Tuscon, Pima County, Arizona.

much smaller, cool weather range near the winter dens at the upper reaches of the arroyos emptying onto the flats. Thus their activity range shifts toward the flats in early summer and toward the foothills in late summer. The greatest distance covered during this annual movement is not known to exceed 2 miles.

The hibernating burrows of the Utah tortoises differ from those farther south in several respects. They are communal and may contain as many as 23 individuals. The burrows attain a length of at least 33 feet, and are frequently divided and anastomosed within, often with multiple openings to the outside (Fig. 25). Each year these dens are slightly enlarged by the scraping of the tenant tortoises preparing for hibernation. The dens are usually on south-facing slopes, generally above the floor of the arroyo, and always in a somewhat cemented gravel.

In both Arizona and Utah the hibernacula are associated with rodent dens. That this is a common and probably important association is fairly clear. It was presumed formerly that the ground squirrels invaded the burrows the tortoises excavated. Studies by the senior author in other parts of southern United States clearly demonstrate that the reverse is the case though pack rats often move in later.

The colder winter temperatures of Utah require longer burrows than in Arizona. Thus it is likely that the anastomosing dens of *G. agassizi* in Utah are simply an extension of the Arizona hibernation situation where the tortoises lie at separate enlarged entrances to a rock squirrel den, but do not enlarge the tunnelways to the end of the rodent labyrinth as they do in Utah. The communal nature of the Utah hibernacula is to be expected in a region that offers fewer sites for adequate winter protection.

In some parts of the range of *G. agassizi*, where winter temperatures are sufficiently cool to require a long burrow and the soil is easily excavated, individuals use a single burrow throughout the year. The tunnel is deeper, but the burrow is otherwise identical to those in Utah the same species uses only in summer (Fig. 25). The regions in which such burrows are found seems to include all the sandy areas in and surrounding the Mohave and Sonora Deserts of California, Arizonia, and northwestern Mexico.

These observations suggest that at least *G. agassizi* and *G. polyphemus* are opportunistic burrowers and excavate a shelter to whatever depth is necessary or possible under prevailing conditions. This behavioral variation is apparently a reflection of several factors. (1)

FIGURE 25. Upper. Communal hibernating burrow of *Gopherus agassizi,* Beaver Dam Slope, Washington County, Utah. Lower. Individual burrow of *G. agassizi* excavated in sandy soil near Mesquite, Washington County, Utah.

the innate behavioral patterns of the species, (2) the local temperature extremes, and (3) the characteristics of the soil in which the retreat is excavated.

As has been shown in the body of this paper, over most of its range *G. berlandieri* has no permanent daily retreat that it uses all year long. With the anterior projection of the plastron the tortoises excavate a shallow form or pallet to which they may or may not return regularly. Though usually little more than a sloping ramp, a few old pallets have the deeper end overhanging enough to cover the entire shell. During winter most individuals bury themselves in the soil. This is the normal pattern on the clayey soils found throughout most of the species' range. On the sandy, less vegetated soils some *berlandieri* dig a longer burrow to which they probably return most of their lives. Others often use burrows of other animals when they are available. Thus this species is as opportunistic as the other members of the genus in shelter construction and excavation.

The pallet of *Gopherus,* and particularly the burrow, has the important function of regulating temperature and moisture, and varies with the season in type, position, and use. In summer the adult *agassizi* often plug their short burrows behind them, obviously an important temperature and moisture regulating device in their desert habitat (Woodbury and Hardy, 1948). We have shown that small *berlandieri* tend to dig proportionately deeper pallets than larger specimens and that they also frequently plug their burrows with earth. In this case shelter depth and the earthen plug are probably related to predation pressure on juveniles as well as temperature maintenance and water conservation.

Our experience shows that of all the *Gopherus* species, *polyphemus* desiccates most rapidly in captivity if deprived of a burrow, which may explain why this species is so consistently associated with burrows throughout almost all its range. The only places where individual *polyphemus* do not dig a burrow are both warm and moist.

Territorial behavior in turtles and tortoises has not been widely studied. None of the principal published studies (Stickel, 1950; Woodbury and Hardy, 1948; Legler, 1960; Cagle, 1944; *et al.*), with the exception of Gould's work on *Terrapene* (1957), demonstrate precisely defined territories or well established homing ability in chelonians. *G. polyphemus* has a rather well-defined activity range within which all feeding and reproduction take place. The populations of *G. agassizi* that retire to burrows instead of pallets show a well-defined home range.

All the evidence available on tortoises indicates positive correlation between individual burrow use and a well-defined home or activity range. For example, throughout most of its range *G. berlandieri* is decidedly nomadic and does not dig burrows. Where it does dig burrows, well-defined trails leading from their entrances show a regular traffic to and from the burrows, in turn suggesting these individuals have a more restricted activity range.

The mean daily movement of individual tortoises, regardless of species, seems greatest in populations where the shelter is apart from the feeding grounds, or where food plants are scarce or widely scattered. Food is plentiful enough in most parts of the range of *G. polyphemus* so that most individuals rarely have to move more than 50 meters from their burrows to feed. On the other hand, individuals of *G. berlandieri* living where food plants are widely scattered may move as much as 400 meters in a day. Such a large activity range is probably not found in those individuals that dig their own burrows, as the extent of their movement is partly determined by the presence of a shelter to which they regularly return. Populations of *G. agassizi* differ greatly in extent of activity range; determined in part by the degree of dependence on a particular shelter, as well as food availability.

No well-developed homing tendency has been demonstrated in the pallet-inhabiting *G. berlandieri,* which probably reflects the relative homogeneity of the activity range with respect to food and shelter. We expect the homing tendency would be better developed in burrow-inhabiting individuals of the same species. The facts that pallets may be used alternately by more than one individual, and that daily activity ranges may overlap quite broadly suggest that lebensraum in this species is not exclusive. Except for those populations whose members live in burrows, apparently very little competition for space and shelter exists in the species.

The most important single factor in population density in *G. berlandieri* is habitat modification by man or other natural agencies. The greatest densities are reached in open brush associations, which are essentially ecotonal. To this extent *G. berlandieri* is identical to the other species of the genus, which also reach their maximum densities in ecotones of a xeric nature.

Within rather broad parameters in the living species of *Gopherus* the fluctuations in the limiting factors of the environment obviously are not nearly so important as the species' regulatory behavioral patterns. This is perhaps best shown in the variability of the type and utilization of shelter. Important in the exact expression of this behavioral pattern are tortoise size, daily and seasonal climatic changes, the extent of plant cover, soil characteristics, and availability of previously excavated shelters of appropriate size and position.

The most significant aspect of the biology of *G. berlandieri* is its behavioral plasticity. An unwritten, but usually implied premise of life history studies is that the particular population studied is assumed to model the behavior and life history of the entire species. We feel that no more reason exists for this assumption than for assuming morphological uniformity throughout the range of a species. In fact the behavioral variation of *G. berlandieri* exceeds the demonstrated degree of morphological variation in this species. Physiological adaptations have certainly determined the range limits of *G. berlandieri*, and within these rather broad parameters the distribution of *G. berlandieri* is a result of behavioral opportunism.

The evolutionary success of tortoises has never really been closely assessed. The protection furnished by the shell is not unique to these organisms. Many other animal groups have developed armor just as effective and in many cases more protective. Nor is major environmental variability an important factor in tortoise evolution. The habitat of virtually all extant tortoise species is very similar, being semiarid grassland or thorn brush. The present investigation of *G. berlandieri* and the accompanying brief review of North American tortoise ecology and behavior presents what we feel is the real basis of evolutionary success witnessed in these organisms. This success stems from a broad, nonspecialized, behavioral base allowing the land tortoise maximum adaptive plasticity through flexible behavioral patterns in order to compensate for seasonal, climatic, and geological changes in the environment.

## CONCLUSIONS

*Gopherus berlandieri* populations on the isolated clay dunes (lomas) near the mouth of the Rio Grande were studied intermittently from 1961 to 1967. The conclusions resulting from this study are as follows:

1. Nests are always excavated in well-drained areas, often under the drip zones of shrubs and in sites relatively free of herbaceous cover.

2. Nests are most common within the areas of greatest tortoise density. Females do not move to special egg-laying areas.

3. Mature females probably lay several egg clutches each year. The number of eggs per clutch varies from 1 to 3, mode 1.

4. The normal pattern of nest construction includes a preliminary stage of nest ramp excavation.

5. Eggs are known to be laid usually from 8 June to 22 August, though some may be laid as late as November.

6. Though raccoons, skunks, and opossums are known egg predators, the southern plains wood rat *(Neotoma micropus)* is perhaps the most active and efficient predator on eggs.

7. In form and color the *G. berlandieri* hatchlings are more similar to those of *G. agassizi* than to those of *G. polyphemus.*

8. Secondary sex characters are apparent at approximately 105 mm in straight line carapace length.

9. Ontogenetic color and pattern changes are not correlated with onset of sexual maturity.

10. The mean shell length of males is greater than that of females.

11. Growth-size increase is greatest the first year after hatching (about 50%), decreases rapidly to sexual maturity at from 3 to 5 years (about 6%), and then slowly thereafter for a period of at least 18 years (about 5%). Females may grow at a somewhat faster rate than males.

12. Mean size is known to vary between populations, probably in response to differences in food and its availability, which are in turn related to the recent geomorphic history of the lomas and human modification.

13. Sex ratios vary from one population to another. The factors governing this variation are not known.

14. Of the several vegetational associations on each loma, tortoise densities are highest in open brush with an understory of grass (1 tortoise: 82 $M^2$). They are least dense in open grass or nonvegetated areas (1 tortoise: 1,575 $M^2$). They do not live in the seasonally flooded tidal flats between the lomas. The high density in open brush is probably correlated with availability of both shelter and food.

15. Daily activity peaks occur in the morning and late afternoon throughout most of the year. Bimodality in activity periods is most pronounced in late summer when midday surface temperatures are high. Unimodality in activity periodicity occurs on warmer days during the winter.

16. No correlation exists between extent or periodicity of movement and sex.

17. Small tortoises move greater distances than larger ones.

18. All individuals tend to maintain a small, temporary activity range, broadly overlapping those of other tortoises, regardless of sex or size.

19. The mean daily movement on the different lomas studied varies widely, and apparently depends on food availability.

20. Yearly movement data show that almost all individulas have a marked nomadic tendency, so that the entire loma may be considered an activity range.

21. Homing ability is not well developed.

22. The cues used in recognition of the transient activity ranges are prabably visual and based on local landmarks.

23. When released on the flats where they do not normally live, in sight of the home loma, tortoises do not necessarily move in its direction, and are apparently completely disoriented.

24. Little interchange of tortoises occurs from loma to loma.

25. Most individuals throughout the species' range excavate a shallow form or pallet in which they spend much of each day and the entire night. Several pallets may be used by one or more tortoises within a particular tortoise activity range.

26. A short burrow is often made in exposed situations on sandy soil. Burrows may be excavated by either the tortoise or by other animals. In some regions burrows are used intermittently, in others continuously. In poorly drained clayey soils, where winter temperatures reach a critical lower limit, the tortoises simply "shuffle" themselves under the surface for protection from the cold.

27. Smaller tortoises tend to dig deeper pallets than larger ones, and frequently plug them with earth behind themselves.

28. The use of pallets in exposed situations varies seasonally.

29. Most commonly eaten are the pads, flowers, and fruits of the cactus *Opuntia lindheimeri* and various grasses. The diet varies seasonally. Many different food items are identifiable by scat analysis. Though essentially herbivorous, coprophagy is common. The young are partly carnivorous, at least in captivity.

30. Food color preference is related to food experience, which varies seasonally and geographically.

31. Predation apparently is highest on the eggs and young. Predators rarely kill adults.

32. The most important single factor affecting tortoise density is habitat modification by either man or natural geologic phenomena.

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