

BULLETIN
OF THE
FLORIDA STATE MUSEUM

BIOLOGICAL SCIENCES

Volume 15

Number 1

**COURTSHIP AND COMBAT BEHAVIOR
IN GOPHERUS BERLANDIERI**

W. G. Weaver, Jr.



UNIVERSITY OF FLORIDA
Gainesville
1970

Numbers of the BULLETIN OF THE FLORIDA STATE MUSEUM are published at irregular intervals. Volumes contain about 300 pages and are not necessarily completed in any one calendar year.

WALTER AUFFENBERG, *Managing Editor*

OLIVER L. AUSTIN, JR., *Editor*

Consultants for this issue:

WALTER AUFFENBERG

CHARLES C. CARPENTER

Communications concerning purchase or exchange of the publication and all manuscripts should be addressed to the Managing Editor of the Bulletin, Florida State Museum, Seagle Building, Gainesville, Florida 32601.

Published 20 March 1970

Price for this issue \$.75

COURTSHIP AND COMBAT BEHAVIOR IN *Gopherus berlandieri*

W. G. WEAVER, JR.¹

SYNOPSIS: Field and laboratory investigations of the courtship and combat behavior of *Gopherus berlandieri* and other *Gopherus* species show that this behavior is specific for each of the two species groups comprising the genus.

In *G. berlandieri* sex recognition is made on the basis of sexually different behavior, cloaca scent, and possibly scents from secretions of seasonally active chin glands found in tortoises only in species of *Gopherus*. Heterosexual preferences by males and females are made only when the chin glands of both sexes are secreting.

Females, but not males, can differentiate sex by cloaca odor and are attracted to other moving tortoises. Neither males nor females can distinguish sex or are attracted to other tortoises by external morphology alone.

TABLE OF CONTENTS

INTRODUCTION	1
ACKNOWLEDGMENTS	3
FOSSIL HISTORY AND SYSTEMATICS OF <i>Gopherus</i>	3
INTERRELATIONSHIPS OF <i>Gopherus</i> BEHAVIOR AND ECOLOGY	4
METHODS	5
BEHAVIORAL AND PHYSIOLOGICAL ELEMENTS IN COURTSHIP AND COMBAT	8
COURTSHIP IN <i>Gopherus berlandieri</i>	18
COURTSHIP IN OTHER <i>Gopherus</i> SPECIES	22
COMBAT IN <i>Gopherus berlandieri</i>	23
COMBAT IN OTHER <i>Gopherus</i>	26
BEHAVIORAL ELEMENTS COMMON TO COURTSHIP AND COMBAT	28
EXPERIMENTS	29
DISCUSSION	36
LITERATURE CITED	41

INTRODUCTION

The acuity of sex and species discrimination in mammals and birds is a function of ecological sympatry with other closely related species and therefore is a behavioral isolating mechanism. Recent

¹The author is an instructor at Miami-Dade Junior College, Miami, Florida, and a research associate of the Florida State Museum. His current research includes vertebrate behavior, ecology, and paleontology. This paper was a Ph.D. dissertation presented to the Graduate Council of the University of Florida in December, 1967.

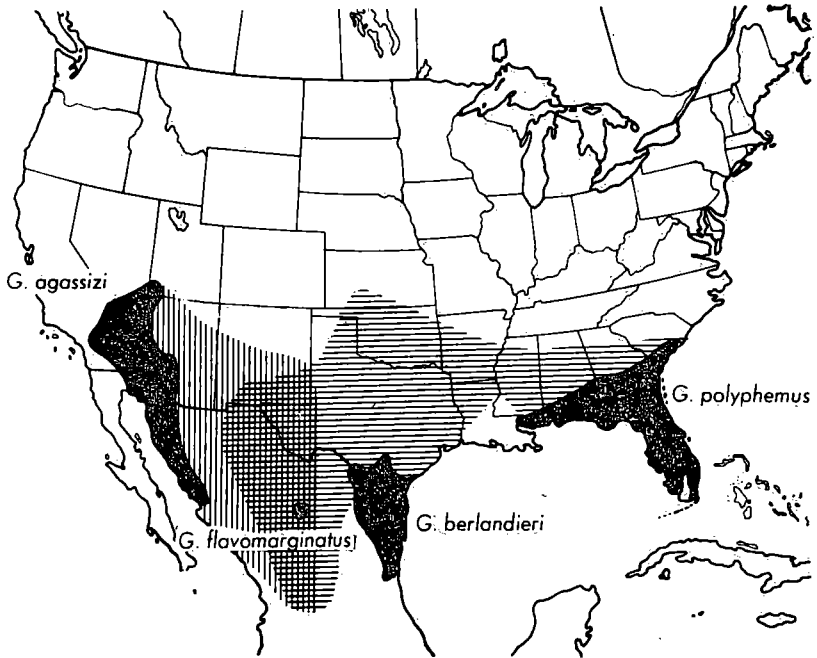


FIGURE 1. Ranges of Pleistocene and Recent *Gopherus* species. Solid black= ranges of extant species. Horizontal lines= Pleistocene range of the *polyphemus* group; vertical lines= Pleistocene range of the *agassizi* group. Squares show area of overlap.

works on fossil and living tortoises suggest that courtship behavior in tortoise species with a long history of sympatry is more complex and discriminating than in allopatric species. A high discriminatory ability may persist in tortoise species currently allopatric, but only in those species pairs whose fossil record reveals a prior sympatry. Sympatric species that are prevented morphologically from interbreeding, such as *Geochelone travancorica* and *G. elegans*, do not have a high discriminatory ability (Auffenberg, 1964b).

The four extant species of the genus *Gopherus* are allopatric, but fossil specimens from northern Mexico and the western United States show that certain species of the genus were sympatric during the Pleistocene (Fig. 1). Thus the extant species provide an opportunity to investigate the influence of prior sympatry (Pleistocene) on the courtship behavior of species that have since become allopatric. The objectives of this investigation are:

- (1) To describe and analyze the courtship and combat behavior of one of these species-*Gopherus berlandieri*;
- (2) To compare this behavior with that known for the other living species of *Gopherus*;
- (3) To search for behavioral elements that have their origin in mutually exclusive courtship patterns resulting from the prior sympatry of *Gopherus* species.

ACKNOWLEDGMENTS

I was helped in this investigation by a grant and facilities from the Welder Wildlife Foundation at Sinton, Texas. A National Science Foundation grant (NSF GB 3738) to Walter Auffenberg partially supported some of the field and laboratory work. The Florida State Museum and the University of Florida Graduate School also provided support. Francis L. Rose provided information and materials for certain sections of this paper. Robert W. Mitchell of Texas Technological College, Lubbock, Texas, generously provided the photograph used in Fig. 5.

I am particularly indebted to Walter Auffenberg whose active interest, unique biological perspective, and personal example guided me throughout the investigation.

FOSSIL HISTORY AND SYSTEMATICS OF *Gopherus*

The earliest known tortoises are represented by fossils from the Eocene of Africa and North America. The earliest North American genus is *Stylemys* from the Eocene (Auffenberg, 1964a). The genus *Gopherus*, a descendant of *Stylemys*, is represented in North America from the Oligocene to the Recent (Hay, 1908; Auffenberg, 1964a). At least as early as the Irvingtonian stage of the Pleistocene *Gopherus* was already divided into its two extant species groups; the *polyphemus* group, and the *agassizi* group (Auffenberg, 1966b). *Gopherus polyphemus* of the southeastern United States and *G. flavo-marginatus* of north central Mexico comprise the *polyphemus* group. *Gopherus agassizi* of the southwestern United States and northwestern Mexico, and *G. berlandieri* of southeastern Texas and northeastern Mexico comprise the *agassizi* group (Fig. 1).

Wermuth and Mertens (1961) consider all living *Gopherus* populations as subspecies of *G. polyphemus*. Most workers (Carr, 1952; Grant, 1960; Auffenberg, 1966b) treat each of the four populations as distinct species, with which I concur.

INTERRELATIONSHIPS OF *Gopherus* BEHAVIOR
AND ECOLOGY

The ecology and habits of only two species of *Gopherus* are reasonably well known. Populations of *G. agassizi* were studied in Utah by Woodbury and Hardy (1948), and *G. berlandieri* has been studied in southeastern Texas (Auffenberg and Weaver, 1969). Additional studies are in progress on *G. polyphemus*.

Individual *Gopherus berlandieri* have no permanent daily retreat as do *G. polyphemus*, *G. flavomarginatus*, and some *G. agassizi*. Over most of the range of *berlandieri* each individual occupies a pallet that is little more than a sloping ramp rarely deep enough to lower the anterior edge of the shell below the surface. The deeper end of older pallets may overhang enough to cover the entire shell. This is the normal shelter on the clayey soils throughout most of the species' range. On more sandy soils some individuals dig a burrow to which they return each day for most of their lives.

All the available evidence on tortoise activity indicates a positive correlation between shelter type and extent of activity range. Where *berlandieri* do not dig burrows they are largely nomadic; burrow-inhabiting individuals maintain a restricted activity range (Auffenberg and Weaver, 1969).

The range of *agassizi* is ecologically more variable than that of the other living species of *Gopherus*. Consequently populations of this species display considerable variation in ecologically related behavior (W. Auffenberg field notes, 1962, 1963, 1964). Individuals in Sonora, Mexico, are nomadic all year, wandering in the region's dry arroyos. Their shelter consists of a hollow scraped into the base of the arroyo wall. Farther north in the vicinity of Pima County, Arizona, the tortoises hibernate in specific winter shelters that are usually enlarged ground squirrel burrows deep enough so that the posterior end of the tortoise's shell is flush with the arroyo wall (Auffenberg, 1969). At the extreme northern end of the range, in the area described by Woodbury and Hardy (1948), the tortoises have different ranges and shelters in summer and winter. In summer they move from the upper reaches of the arroyos onto the flats where they excavate short burrows. In winter they hibernate in communal burrows excavated in the arroyo walls. The seasonal changes of shelter are accompanied by seasonal changes of activity ranges; the summer and winter ranges do not overlap.

G. polyphemus usually lives on sandy soil where it digs a long, usually nonbranched burrow. Adults may build new burrows, but

normally each individual uses a single burrow throughout its life. Thus individual *polyphemus* have restricted activity ranges (Auffenberg, 1969).

Very little is known of *flavomarginatus*, except that it excavates burrows in the playa soils of the Chihuahuan desert community in Mexico.

The presence or absence of an individual activity range has an effect on courtship. Tortoises such as *polyphemus* that have individual activity ranges must leave their customary area in order to mate. Nomadic tortoises such as *berlandieri* regularly make contact with other tortoises. Therefore the portion of courtship involved in finding the opposite sex might be expected to differ in each of the above circumstances.

METHODS

The courtship and combat behavior of *G. berlandieri* was investigated in both field and laboratory. A total of 103 days of field work was begun in November 1963, and completed in October 1967.

These tortoises are nomadic, small, shy, and reach maximum population densities in relatively thick, thorny brush. Many days were spent in the field without seeing courtship or combat, yet this paper represents the most intensive investigation of tortoise courtship and combat behavior published.

Laboratory experiments were designed to analyze behavior sequences, especially the nature and importance of the cues *berlandieri* uses to distinguish sex in its own species. I rejected the idea of making the study entirely experimental. Observations of such complex behavioral interactions as courtship and combat made only on captive animals do not necessarily reflect accurately similar behavior in nature (Carpenter, 1962). My experiences have shown that tortoises kept together soon become accustomed to one another with a resulting reduction in the frequency of courtship or combat activity. Such tortoises evince renewed courtship or combat behavior when strange individuals are introduced.

The field work revealed that species-specific head movements and olfactory stimuli are the chief releasers for courtship and combat. The front and rear portions of the tortoise are the most likely sources of olfactory cues relating to sex and species identification. The specific sources of odoriferous materials proved to be the chin glands (described in a later section) at the animal's anterior end and the cloaca at the posterior end. Cloacal scent is known to be important in sex

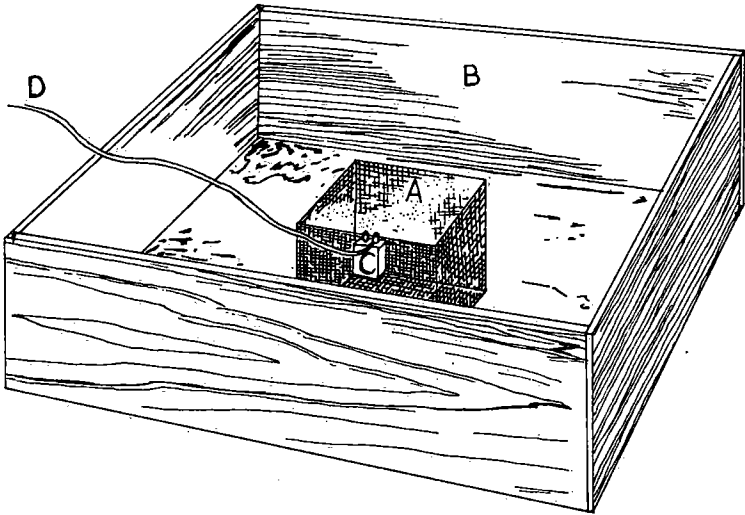


FIGURE 2. The open square apparatus. A, removable cage. B, pen (5' x 5' x 18") containing experimental tortoise. C, vacuum tube sensor. D, wire leads from sensor to digital counter.

discrimination in *Geochelone carbonaria* and *G. denticulata* (Auffenberg, 1965). Movements of the tortoise are potentially important visual cues. Experiments with *G. berlandieri* were designed to investigate the roles of odors from the cloacal and chin glands and tortoise movements in courtship and combat behavior. The following experimental devices were used:

THE OPEN SQUARE.—These tests provided data on differential responses between male and female tortoises to other male and female tortoises and to controls. The test apparatus (Fig. 2) consisted of an open-topped box with a wire screen floor. In the center of the floor was a square of felt. A small, removable cage with wire sides was placed on rubber mats within the felt square. A Grayson-Stadler vacuum-switch-sensor (Model E4690L) was attached to one of the wire sides of the small cage with leads to a digital counter and a Grayson-Stadler drinkometer panel counter (Models E4690A-1 and #3700A, respectively). The switch operated on a 0.06 millivolt differential, which apparently was not detectable by the tortoises and assured maximum sensitivity. When the tortoise, grounded by the screen on the floor and the dampened felt, touched the wire sides of the small cage, it closed the sensor circuit. The digital counter recorded each closure.

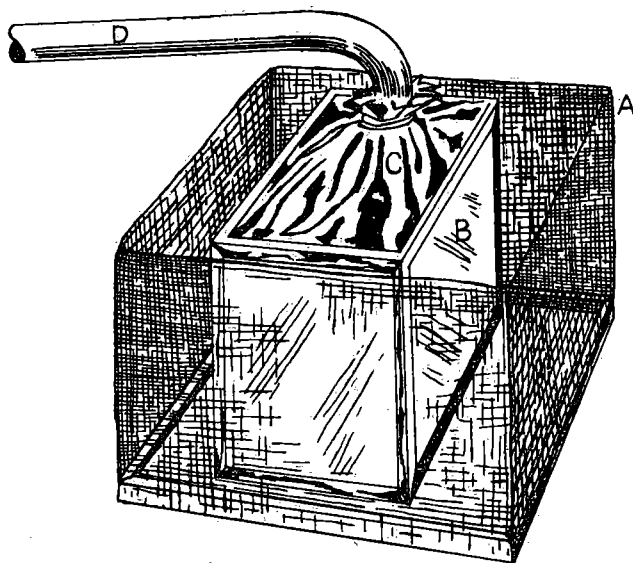


FIGURE 3. The closed square apparatus. A, removable cage. B, 5-gallon aquarium. C, airtight plastic seal. D, hose providing air to stimulate tortoise.

THE CLOSED SQUARE.—Live and preserved tortoises were used as stimuli to test the responses of male and female tortoises to the sight and movement of other male and female tortoises. The closed square apparatus was the same as that of the open square with the addition of an aquarium placed inside of the small, removable cage (Fig. 3). The aquarium was sealed with a plastic bag fitted around a wooden frame attached to the top of the aquarium. A long plastic hose provided air.

THE SCENT CHAMBER.—A metal-bottomed cage (Fig. 4) served as a chamber for testing reactions to scents. Glass jars with wire fronts were recessed into the front wall. One Grayson-Stadler sensor was connected to the front of each jar. Samples of potentially important odoriferous material were placed in the jars. An electrical circuit was closed when a tortoise's nose touched the jar's wire front.

HORMONE INJECTIONS.—Thyroxine, progesterone, and testosterone were injected subcutaneously to certain individuals in an effort to stimulate courtship or combat behavior and to evaluate the role of the hormones in the functioning of the chin glands (described below) found in *Gopherus* species and believed to influence courtship and combat behavior.

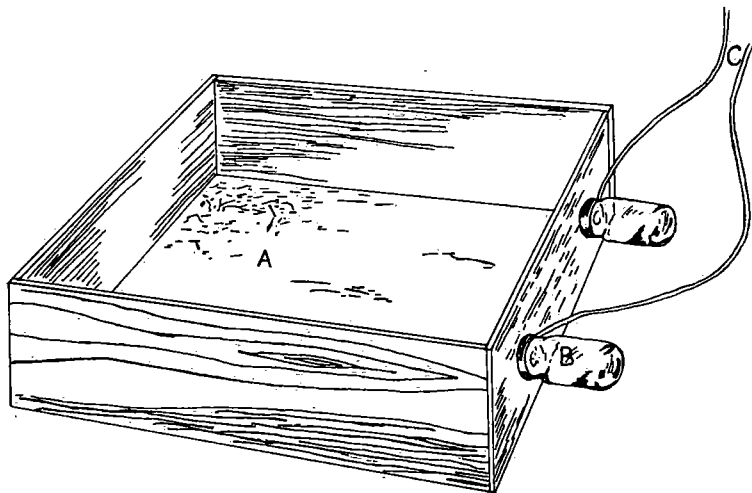


FIGURE 4. Scent testing chamber A, cage (6' x 4' x 1'). B, jars containing odor stimuli. C, leads to sensor and digital counters.

PHOTOGRAPHS.—Tortoises engaged in various aspects of courtship and combat behavior were photographed on both 8 mm and 16 mm motion picture film. Many 35 mm photographs were taken, particularly in the field. Both the motion pictures and still photographs served to evaluate the type and extent of each behavioral element in courtship and combat behavior.

BEHAVIORAL AND PHYSIOLOGICAL ELEMENTS IN COURTSHIP AND COMBAT

As in other animals the reproductive activities of *Gopherus berlandieri* are an interaction of physiological and behavioral elements. While the scope of this paper is not to trace the major hormonal and other chemical changes affecting courtship and combat behavior, one such aspect in *berlandieri* is of relevance here. From the start of this investigation in November 1963, field observations of *berlandieri* suggested that breeding behavior in this species seemed to be correlated with the enlargement of a pair of large integumentary glands located ventrally and slightly medially on each mandibular ramus (Fig. 5).

Among tortoises these glands are known only in species of *Gopherus*. Smith and Brown (1946) reported them as being found only in *G. berlandieri* and interpreted them as degenerate capsules of connective tissue, but in his description of *berlandieri* Agassiz

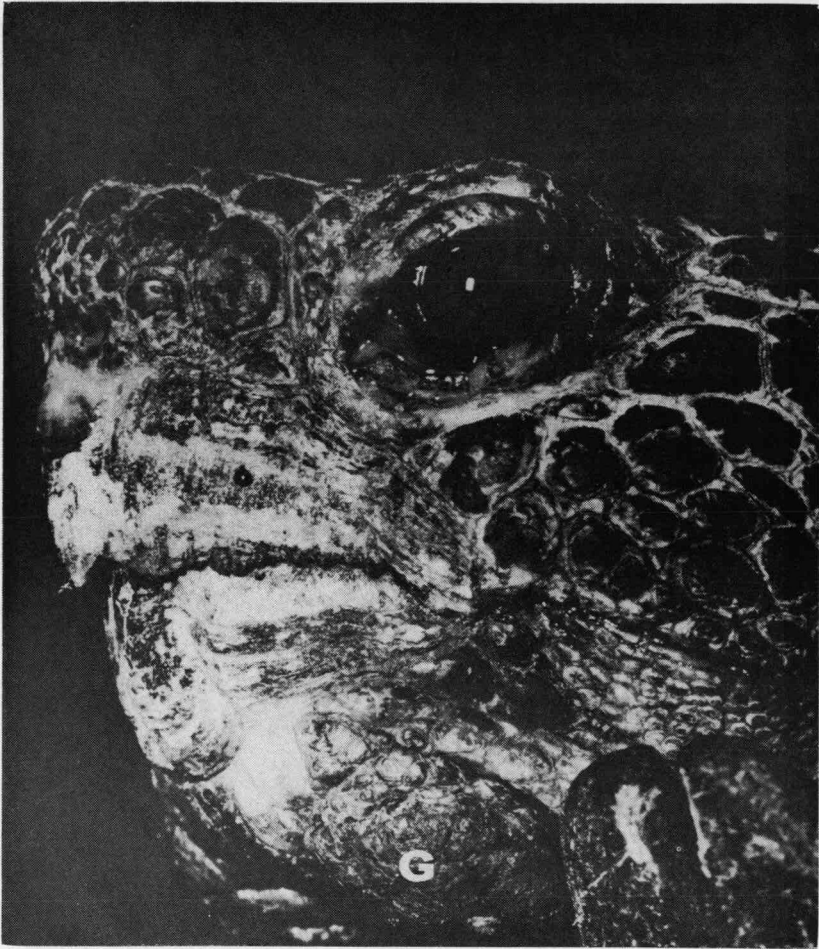


FIGURE 5. External view of actively secreting chin glands. G, of a male *Gopherus berlandieri*.

(1857) compared its chin glands with the similar glands of *G. polyphemus*. Grant (1936) had already reported chin glands in *G. agassizi*, and later Legler and Webb (1961) described them in *G. flavomarginatus*. Chin glands are well known in rabbits, where their secretion is used to mark territorial boundaries (Mykytowycz, 1965). In *Gopherus* the glands are larger in males than in females, and larger in *agassizi* and *berlandieri* than in *polyphemus* or *flavomarginatus*.

Auffenberg (1966a) found that female *polyphemus* rubbed their

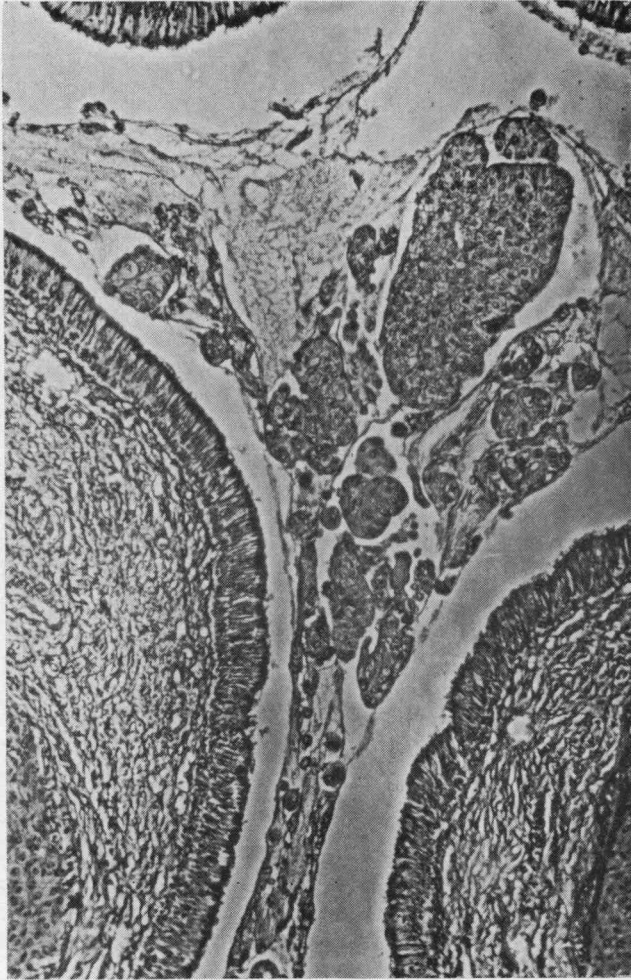


FIGURE 6. Histological section from the chin gland of a male *Gopherus berlandieri* made in November 1966, showing collecting duct lined with epithelial cells. The mass in the duct is composed of cells that have built up their products and have been discharged into the lumen as is typical of holocrine glands. The base of the gland is at the bottom of the photograph.

forearms against the jaw in the region of the glands during courtship, and I have noted similar behavior by male *polyphemus*. All species of *Gopherus* have an enlarged scale on the forearm in the proper position to be rubbed across the gland; this scale is best developed in *polyphemus* and *flavomarginatus*. Investigations of the

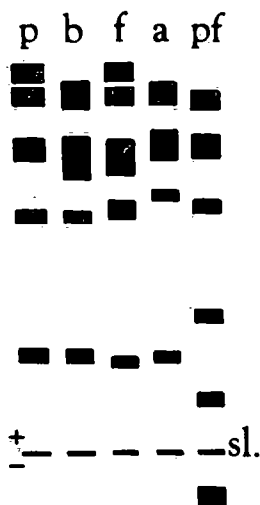


FIGURE 7. Graphical representation of starch gel electropherogram of chin gland proteins. p, male *G. polyphemus*; b, male *G. berlandieri*; f, male *G. flavomarginatus*; a, male *G. agassizi*; pf, female *G. polyphemus*; sl, application slots. After Rose, *et al.*, 1969.

gland's histological properties (Fig. 6) and electrophoretic analyses of its secretion were begun in January 1967 (Rose, *et al.*, 1969). Histological examinations showed them to be functional in both males and females and similar in structure to mammalian sebaceous glands. They open to the outside by two or three ducts, and their secretory activity varies seasonally. In the Brownsville, Texas, region the glands of adult males begin to enlarge in June, and by July they are fully enlarged in adults of both sexes. In nature the glands of specimens from this population remain enlarged at least until December. Most specimens maintained in an indoor pen on a 15-hour day had the glands enlarged until early January; by the end of January the glands had receded in most of the tortoises. These tortoises were moved to a large outdoor pen in Gainesville, Florida on 1 February 1967. A week later the glands of all these tortoises had receded fully and no secretory material was obtainable when the glands were gently squeezed as in previous months.

Electrophoretic analyses of the glandular secretions in species of *Gopherus* show that the secretion contains proteins, an esterase, and three classes of lipids. The lipid classes are triglycerides, fatty acids, and a steroid, cholesterol. Interspecific variation exists in the number of esterase bands and in the proteins present in the secretion. The

Table 1. BEHAVIORAL ELEMENTS IN TORTOISE COURTSHIP AND COMBAT

Head bobbing	<i>Geochelone travancorica</i> (Auffenberg, 1964b) <i>G. carbonaria</i> (Snedigar and Rokosky, 1950; Auffenberg, 1965). <i>G. denticulata</i> (Auffenberg, 1965) <i>Gopherus agassizi</i> (Woodbury and Hardy, 1948; Nichols, 1957) <i>G. berlandieri</i> (Householder, 1950) <i>G. flavomarginatus</i> (Legler and Webb, 1961) <i>G. polyphemus</i> (Auffenberg, 1966a)
Trailing	<i>Geochelone carbonaria</i> (Snedigar and Rokosky, 1950) <i>G. elephantopus</i> (Watson, 1962) <i>G. pardalis</i> (Watson, 1962) <i>Gopherus agassizi</i> (Nichols, 1957) <i>G. berlandieri</i> (Hamilton, 1944) <i>G. flavomarginatus</i> (Legler and Webb, 1961) <i>G. polyphemus</i> (Auffenberg, 1966a) <i>Homopus areolatus</i> (Eglis, 1963)
Courtship position	<i>Homopus areolatus</i> (Eglis, 1962)
Smelling	<i>Geochelone carbonaria</i> (Auffenberg, 1965) <i>G. denticulata</i> (Auffenberg, 1965) <i>Gopherus agassizi</i> (Camp, 1916) <i>G. berlandieri</i> (Householder, 1950) <i>G. polyphemus</i> (Auffenberg, 1966a) <i>Homopus areolatus</i> (Eglis, 1963)
Biting	<i>Chersine angulata</i> (Rose, 1950) <i>Geochelone denticulata</i> (Beltz, 1954) <i>G. elephantopus</i> (Heller, 1903) <i>Gopherus agassizi</i> (Camp, 1916; Grant, 1946; Woodbury and Hardy, 1948) <i>G. berlandieri</i> (Householder, 1950) <i>G. polyphemus</i> (Auffenberg, 1966a) <i>Homopus areolatus</i> (Eglis, 1963) <i>Testudo graeca</i> (Doumerque, 1899; Nikolskii, 1915; Watson, 1962)
Ramming	<i>Chersine angulata</i> (Rose, 1950) <i>Geochelone carbonaria</i> (Auffenberg, 1965) <i>G. denticulata</i> (Beltz, 1954; Auffenberg, 1965) <i>G. elephantopus</i> (Ditmars, 1910; DeSola, 1930) <i>G. oculifera</i> (FitzSimons, 1935) <i>G. travancorica</i> (Auffenberg, 1964b) <i>Gopherus agassizi</i> (Miller, 1932; Nichols, 1953) <i>G. flavomarginatus</i> (Legler and Webb, 1961) <i>G. polyphemus</i> (Carr, 1952) <i>Testudo graeca</i> (Nikolskii, 1915; Watson, 1962)

Circular movement of courting pair

- Gopherus agassizi* (Woodbury and Hardy, 1948)
G. polyphemus (Auffenberg, 1966a)
Homopus areolatus (Eglis, 1963)

Vocalization

- Geochelone carbonaria* (Snedigar and Rokosky, 1950)
G. denticulata (Grant and DeSola, 1934)
G. elephantopus (Heller, 1903; DeSola, 1930; Watson, 1962)
G. oculifera (FitzSimons, 1935)
G. pardalis (Watson, 1962)
Gopherus berlandieri (Householder, 1950)
Testudo graeca (Nikolskii, 1915; Watson, 1962)

Presentation

- Geochelone elephantopus* (DeSola, 1930)
Gopherus agassizi (Householder, 1950)
G. polyphemus (Auffenberg, 1966a)

protein concentration of the secretion in females of all *Gopherus* species is much lower than in males. Females, but not males, of all *Gopherus* species have a cathodal migrating band (Fig. 7).

Tortoise courtship and combat consist of complex series of behavioral interactions. The particular sequence of these elements varies interspecifically, and some elements are absent in some species. Certain behavioral elements have been recorded frequently enough in different and unrelated species to imply the existence of a generalized type of tortoise courtship or combat consisting of common behavioral elements. Table 1 lists nine behavioral elements of courtship or combat behavior found in *Gopherus* species and the other tortoises in which each element has been reported. At present more courtship and combat behavior is known for *Gopherus* species than for any other tortoise species. Thus *Gopherus* is used here as a standard for comparing behavior in other tortoise species.

HEAD BOBBING.—Eglis (1962) recognizes head movements in tortoises as either "latolent" (lateral) or "dirolent" (straight). He states that head bobbing of living species of *Gopherus* is basically straight: the neck is usually fully extended and the head is nodded vertically. Figure 8 shows the duration and frequency of the vertical aspect of head bobbing in individuals of three *Gopherus* species.

Individuals of all species of *Gopherus* bob their head when smelling objects such as food. Bobbing also occurs in meetings between two or more tortoises, and in individuals of *Gopherus* it reaches its greatest frequency during courtship and combat. In courtship the male bobs more actively than the female. Low intensity bobbing is

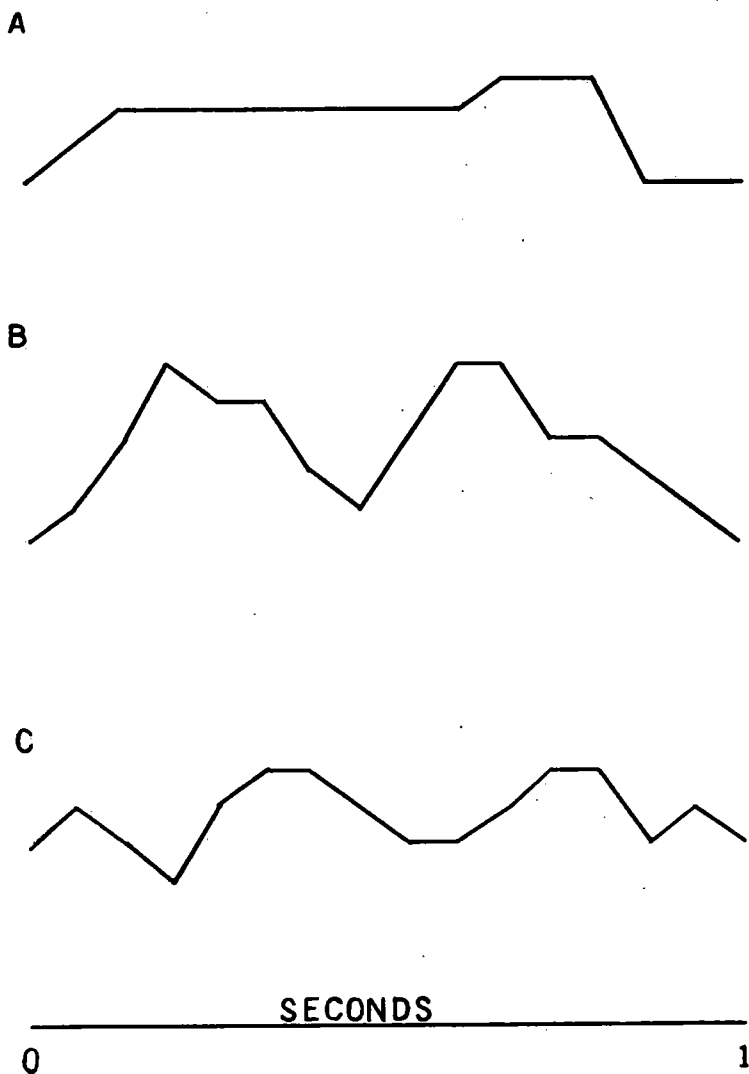


FIGURE 8. Action patterns of head bobbing. A, *G. berlandieri*. B, *G. agassizi*. C, *G. polyphemus*.

performed with the head not fully extended. Bobbing-like movements may be observed when the head is nearly retracted, but these result from breathing and not olfaction. Head bobbing sequences vary in length and have no discernible pattern correlated with either sex or species in *Gopherus*, except that the sequences are usu-

ally longer during social interactions than when food or feces are being sniffed. The bobs performed in courtship and combat are apparently identical. One clearly demonstrated function of head bobbing in tortoises occurs in *Geochelone carbonaria* and *G. denticulata* (in which the head movement is lateral) where it acts as a species-specific visual signal (Auffenberg, 1965).

TRAILING.—This behavioral element (Table 2, Stage 1) marks the start of courtship, and to a lesser extent combat. A male trails either a female in courtship or a male in combat. At the beginning of courtship or combat in *G. berlandieri*, the male walks 3 to 10 feet behind the female for as long as an hour with his head extended, bobbing at irregular intervals. Male *berlandieri* make no attempt to overtake the female during this early stage. The rate of the female's activity influences that of the male; if she stops, he stops. The male's attention is directed toward the female, and his behavior is dependent on hers. She often grazes during this period. In the courtship of *G. polyphemus* the female is more aggressive and may walk toward the male. Obviously trailing will eventually bring the male and female together physically, and the significance of its ritual-like cadence in the early part of courtship in *G. berlandieri* is unknown.

Eglis (1963) reported an instance of a male *Homopus areolatus* following a female in a peculiar manner: his front feet were limp, and he progressed by pushing with the rear feet.

COURTSHIP AND COMBAT POSITIONS.—A characteristic courtship stance has been reported only for *Homopus areolatus*, in which the male and female face each other with their shells at a 90° angle (Eglis, 1963). This positioning is accomplished by the male's rushing around first one side and then the other of the female. I have noted similar positioning in confrontation between captive male *Gopherus polyphemus*; the stance assumed by the aggressive tortoise is more dependent on the timidity of the nonaggressive male than on strenuous efforts by the aggressive male as in *Homopus areolatus*. No similar positioning has been reported for other species of *Gopherus*, nor have I observed any.

OLFACTION.—Male tortoises sniff various portions of females or other males in all courtship and combat encounters I have watched, and in those reported in detail in the literature. The movement associated with olfaction in *Gopherus* is the head bob. Head bobbing in most courtship or combat situations differs in minor but consistent ways from that when food or feces are being sniffed. These latter movements in *Gopherus* have a predominant forward motion. Olfac-

tion in *Gopherus* is a simple straight forward motion with little of the vertical component that essentially characterizes head bobbing as seen in courtship or combat. Thus a distinction exists between the types of head movements performed when odor is the only stimulus, as opposed to the head movements in the head bobbing of courtship or combat. During meetings between tortoises head bobbing of the kind observed when food or feces are examined occur repeatedly. In these sniffing movements the head is directed toward the front or rear portions of the other tortoise.

BITING.—Biting occurs in both courtship and combat in *G. berlandieri*. I have never seen biting in combat by *G. polyphemus*, but it occurs in the combat of *G. agassizi* (Table 1). During courtship *berlandieri* males bite the females on the head, front legs, and the front edge of the carapace. As courtship proceeds biting becomes increasingly confined to the anterior edge of the female's carapace. In *berlandieri* biting also occurs in combat. Both males may bite one another forcibly, although I have never seen injuries. During courtship in *polyphemus* the males bite the head and front feet of the females, but confine most of the shell biting to the female's gular projection; the anterior carapace edge is not bitten. Camp (1916) and Woodbury and Hardy (1948) report biting in both courtship and combat of *G. agassizi*. Eglis (1963) reports that a courting male *Homopus areolatus* bit a female's head vigorously. I have seen female *Geochelone elephantopus* produce serious wounds by biting exposed areas of *Gopherus polyphemus*, although the biting was not in a courtship or combat context. Beltz (1954) reports that a male *Geochelone denticulata* attacked a large *Gopherus agassizi* by biting and ramming its shell and limbs. Biting in tortoise courtship is not universal, and at least one species, *Geochelone travancorica*, courts without biting (Auffenberg, 1964b).

RAMMING.—The male rams the female during courtship in all tortoise species whose courtship is well reported. In *berlandieri* courtship the male rams the female's sides more frequently than other parts of her shell. Ramming in combat is centered on the front ends of the shells of the opposing males. Combat ramming often develops into a pushing contest. One male attempts to place his gular projection under the plastron of the other and to overturn him with a distinctive upward thrust at the end of each ramming movement. This upward thrust is missing from *berlandieri* courtship ramming. In combat the ramming motion begins with the tortoise standing on all four legs and is initiated by a slight backward rocking movement,

followed immediately by a sudden forward thrust in which the head and, to a lesser extent, the front legs are withdrawn. The withdrawal of the front legs gives the forward thrust a downward angle. Immediately after impact the front legs are extended fully, thus providing the characteristic upward arc. In courtship ramming the front legs do not appear to be withdrawn, there is no upward arc at the end of the forward thrust, and the ramming movement is more horizontal. In *Gopherus* and other tortoises the function of ramming is to immobilize the female in courtship and the male in combat.

Watson (1962) reports a rhythmic quality in the ramming of female *Testudo graeca ibera* by the male that I have not noted in any species of *Gopherus*. Ditmars (1910) reports a peculiar lateral bumping in the courtship of *Geochelone elephantopus*, but does not describe clearly just how it was accomplished.

LOCOMOTION.—During certain phases of courtship in *G. berlandieri*, *polyphemus*, and *agassizi* the female appears to avoid a face to face confrontation with the male by retreating. Her path of retreat is usually circular or semicircular, as the male charges, bites, and rams her first from one side and then the other, always trying to meet her head on. Thus in *berlandieri* the courting pair move circularly, the male in an outer, larger circle and the female in an inner, smaller one. In combat between some male *berlandieri* a similar circular retreat pattern arises when the less aggressive male tries to avoid the more aggressive male and thus occupies the inner circle. In *polyphemus* courtship the female avoids the male by a similar retreat pattern.

In *Homopus* the male circles the female to ram or bite her, but she does not avoid him by turning away in the circular path described for *Gopherus*, but would "agitatedly skitter aside" (Eglis, 1962).

VOCALIZATION.—Vocalization has been reported for several tortoise species during courtship or copulation, but not during combat. Van Denburgh's (1914) account of vocalization by *Geochelone elephantopus* during combat has been questioned (Auffenberg, 1965). In *Gopherus* it has been described for *berlandieri* by Householder (1950) whose description was based on a courtship between two tortoises he presumed were desert tortoises, *G. agassizi*; Woodbury (1952) later showed that the male of this pair was actually a Texas *berlandieri*. Campbell and Evans (1967) report vocalization in *G. agassizi*, but not in a courtship or combat context. Most reports of vocalizing during breeding activities suggest the sounds are a by-product of the copulatory effort; nothing indicates that they serve

as an auditory signal. Yet Van Denburgh (1914) reports that *Geochelone elephantopus* males bellow before copulation, and Snedigar and Rokosky (1950) report the same by males of *G. carbonaria*. (This latter observation was made presumably on *Geochelone denticulata*, but the accompanying photograph clearly shows the tortoises to be *G. carbonaria*.)

PRESENTATION.—A female invites copulation and facilitates successful intromission in higher vertebrates by presenting. In *G. berlandieri* the female holds her body in a characteristic position with head and forelimbs withdrawn and rear limbs partially extended, and extrudes her cloaca. In *polyphemus* the presentation is similar, but the female's rear legs seem to be extended more stiffly than in *berlandieri* and she may pivot so that the rear of her shell is nearest the males head, which I have never seen in *berlandieri*.

COURTSHIP IN *Gopherus berlandieri*

I studied courtship afield in Texas near Brownsville in Cameron County and near Laredo in Webb County. My earliest observations

TABLE 2. STAGES OF COURTSHIP OBSERVED IN *Gopherus berlandieri*

Stage	Male	Female
1.	Follows female and occasionally bobs head Increased vigor of head bobbing, rate of walking surpasses that of female	Indifferent to male
2.	Overtakes female, bites her feet, carapace	Increases walking speed
	Rams female	Tries to avoid male, turns away from him, both describe a circular pattern
		Withdraws head and front feet, rear feet remain extended
3.	Initial mounting attempts	Remain still, or may attempt to walk away
	Rams and bites if female tries to walk away	
4.	Coition	

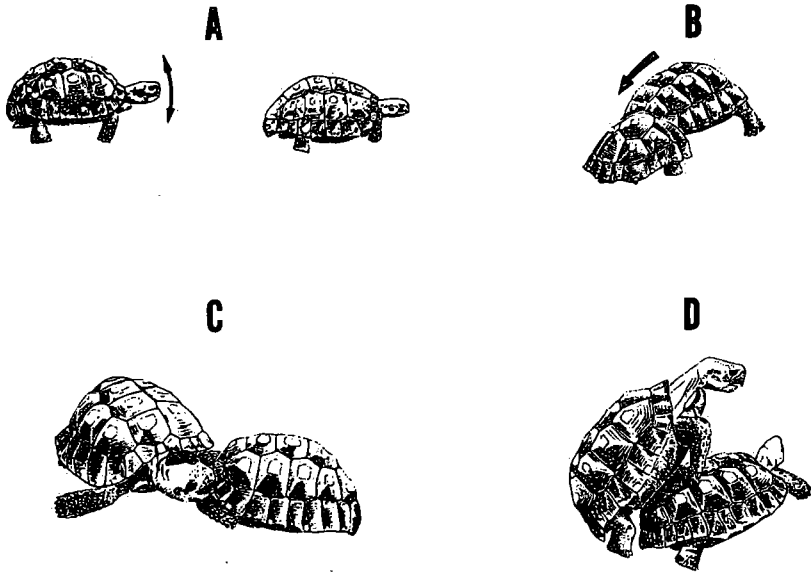


FIGURE 9. Stages of courtship in *Gopherus berlandieri*. A, trailing. B, ramming. C, biting. D, mounting.

of courtship were in June, and the latest in November. I also watched courtship in outdoor enclosures at the Welder Wildlife Refuge near Sinton, San Patricio County, Texas, and at Gainesville, Florida. I recorded 12 complete courtship sequences in the field and approximately 12 incomplete performances (less than three of the four stages in Table 2) in the field and among captive specimens.

Behavior preceding copulation can be treated in four stages (Table 2). Stage one is a relatively passive phase during which the female shows little active response to the male's presence, but during which she modulates his behavior. In the remaining stages the female's behavior is modulated by the male's.

STAGE ONE.—Courtship behavior begins by the male trailing a female (Fig. 9A). Initially he walks 3 to 10 feet behind her, and his behavior is modulated by hers as two major characteristics of the trailing stage show: (1) he stops whenever she stops, and (2) he often bobs his head in her direction. During the early portion of the trailing stage the male usually walks with his neck only partly extended. During this initial stage of courtship the female's behavioral role is largely one of indifference and she does not bob her head at any time. She normally grazes and "noses" at various items on the

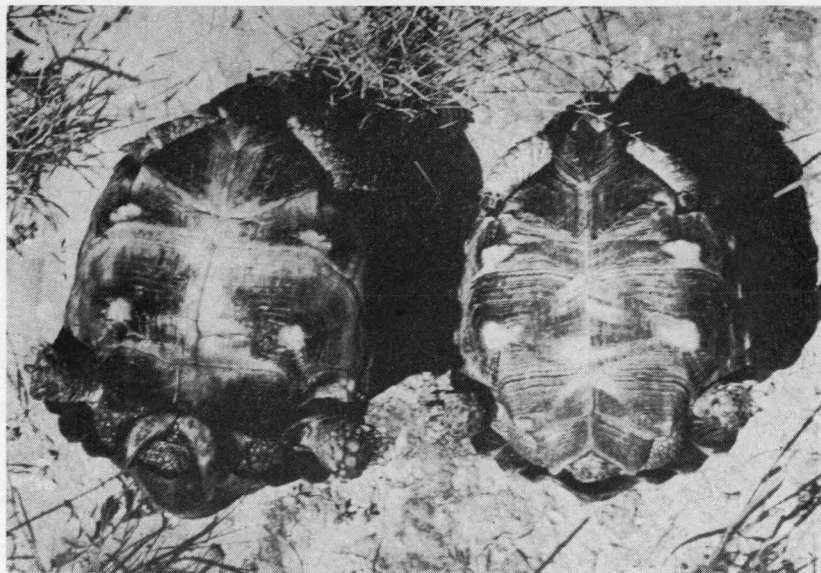


FIGURE 10. Sexual dimorphism in *Gopherus berlandieri*. Males (left) have a deep posterior plastral depression, thickened anal notch margins, and an elongate gular projection at the anterior end. The female's plastron (right) is flat without thickened anal notch margins and has a shorter gular projection. The posterior ends of both tortoises are at the bottom of the photograph.

ground, displaying the same movements and activity as lone, unattended females do. Occasionally she makes one or more stops in the shade, during which the male appears to lose interest and may even graze. When she resumes walking, the male continues his trailing. These shade stops may be temperature regulating behavior.

Late in the trailing stage, which may last from a few minutes to nearly an hour, the male shortens the distance between himself and the female. When he is about 3 feet directly behind her he increases the frequency and vigor of head bobbing and when not bobbing holds his head parallel to the ground in a high, arched position, his neck inclined between 25° and 35° . At this point the female increases her walking speed, and ceases all grazing. This shift in the female's behavior marks the end of stage one.

STAGE TWO.—The second stage of courtship marking the start of phase two is more intense than the first, and begins when the male tries to overtake the female and confront her face to face. On overtaking her he stops her by biting her head, front feet, and the top

front edge of her carapace, and ramming her forcibly with his massive, elongate gular projection (Fig. 9 B, C; Fig. 10). The female at first avoids him by turning away from him so that both tortoises move in a circular path of constantly diminishing diameter. As the male increases the intensity of his biting and ramming, the female finally withdraws her head and front legs but continues to pivot her anterior end away from him by driving with her rear feet. With his increased biting tempo, the male's head bobbing stops or loses any recognizable pattern, and he increasingly confines his biting to the female's nuchal and anterior peripheral bones. The bites now become quite forceful, the male often grasping the female's shell in his mouth and alternately pushing and pulling her, and she soon withdraws her head and front feet, leaving her rear feet extended so she is in an incline with the rear of her shell highest. She no longer pivots, and the male attempts to mount her. The stimulus or releaser for mounting behavior in the male seems to be the female's inclined position. Observations Walter Auffenberg made near Laredo, Texas suggest that the female selects the place where stage two and the subsequent stages occur, usually one relatively free of underbrush.

STAGE THREE.—The male may try to mount from any place on the female's shell. If the initial attempts occur at other than the rear of the female's shell, he works his way to the rear with his front feet on the dorsal surface of her carapace and his rear feet on the ground (Fig. 9D).

STAGE FOUR.—None of the unions I observed lasted over 10 minutes and were terminated when the female walked out from under the male. Householder (1950) reported that a female *berlandieri* (which he thought was a female *agassizi*) everted part of her cloaca, apparently to facilitate intromission by the male. This occurs in female *polyphemus* and Eglis reports it in *Homopus*, but I did not witness it in *berlandieri* courtships.

Each thrust by the male during copulation pushes the female forward. To compensate for her change of position the male performs a series of hopping steps with his rear feet. Occasionally his rear legs become tangled in grass, which impedes his hop-stepping and interrupts copulation. Thus the female's selection of a relatively clear area helps ensure successful coition.

I watched one pair trailing (Table 2, Stage 1) on the northeast side of one of the lomas (dunes) characteristic of the Jackass Prairie, near Brownsville, Texas, from 19:00 until 20:00. The male, bobbing his head in series of between 3 and 36 bobs, stopped when the fe-

male stopped. Twice during this sequence the individuals faced one another at approximately 110° and the male's head was in the female's field of vision, but she did not reciprocate with head bobs. Just before dark (19:30) she stopped in an open space with scattered clumps of grass (*Bouteloua*) and prickly pear (*Opuntia*), headed into a clump of grass, and came to a halt. The male stopped both walking and head bobbing. The female withdrew head and feet. The male's head protruded about $1\frac{1}{2}$ inches. Both were still in these positions when I left at 20:00.

When I returned at 05:15, the tortoises were in the same place and in the same positions as when I left them. At 07:10 the male extended his neck fully at an angle of about 20° and resumed bobbing in sequences averaging seven bobs, but his head was not in the high arc I observed in other courtships. By 07:27 neither tortoise had moved from where they had stopped the previous night, and the male began to hold his head in the high arched position. At 07:35 the female started to walk and the male followed immediately bobbing his head. By 07:40 the male skirted the female on her right. She turned away from him counter-clockwise and he followed, still bobbing. He bit the anterior end of her shell and she withdrew her head and forefeet. By 07:45 she was no longer turning away from him, his bites were more forceful, and he grasped, pushed, and pulled her. At 07:50 he mounted and held his mouth open during copulation. I heard no sounds from him, but both the wind direction and my being 30 yards away may have dampened any vocalization. At 07:58 the female walked out from under him. He followed her for 5 or 6 feet and made a few slow, low intensity head bobs. She moved into a pallet, and he walked away.

COURTSHIP IN OTHER *Gopherus* SPECIES

The courtship of *G. polyphemus* as described by Auffenberg (1966a) differs in several respects from that of *berlandieri*. In no instance have I seen female *berlandieri* initiate courtship as *G. polyphemus* (Table 3, Stage 2). Head bobbing is faster in *polyphemus* than in *berlandieri* (Fig. 8). Ramming of the female by the male is similar in both species, but the biting (Table 3, Stage 3) differs in that *berlandieri* males do not bite the female's gular projection. In the two species courtship is similar in that the female moves backward away from the male in a circular path during the biting phase (Table 2, Stage 2; Table 3, Stage 4).

The only reference to courtship or combat behavior in *G. flavo-*

TABLE 3. STAGES IN THE COURTSHIP OF *Gopherus polyphemus*¹

Stage	Male	Female
1.	Walks in circle and bobs head	Approaches male
2.	Bobs head violently with approach of female	
3.	Bites female on legs and shell especially gular projection	Moves backward in semi-circle; stretches hind legs
4.	First mounting attempts (usually unsuccessful) followed by more biting	
		Radius of semicircle becomes so small that female begins to pivot 180° about a central point
5.	First successful mountings and finally coition	

¹After Auffenberg (1966a).

marginatus is by Legler and Webb (1961), who note that males initiate courtship and that the females do not approach males as in *polyphemus*. Male and female *flavomarginatus* tend to push or crowd other tortoises against an object such as a fence post or rock. In one instance a female *flavomarginatus* crushed a female and on another occasion a male *polyphemus* against a fence post so forcibly that the shell of the *polyphemus* was fractured in several places (Francis L. Rose, pers. comm.).

Courtship observations on *agassizi* are numerous but are lacking in detail. Householder (1950) provides a good account of successful courtship in what he assumed was *agassizi*, but as noted above was actually between a male *berlandieri* and a female *agassizi*. Woodbury and Hardy (1948) describe a courtship (?) of *agassizi*, but with too few details to compare with the behavior in other species. Tortoise behavior varies in significant but often extremely subtle ways, as does tortoise morphology, and to study it we need meticulous descriptions of all its phases.

COMBAT IN *Gopherus berlandieri*

Combat in *berlandieri* occurs only between males. One observed instance of agonistic behavior between females involved only push-

ing. Combat begins before the breeding season and declines sharply in frequency before the breeding season ends. The following notes are based on three complete and four partial combat sequences seen in the field and on many partial sequences watched among captive tortoises. I have seen combat between captive males kept in an outdoor pen in Gainesville as early as March 12 and in the field as late as July.

Two aggressive males approach each other and ram. One combatant attempts to overturn the other. One male walks toward the other, or both move toward each other. Their heads may be motionless or bobbing vigorously. At first ramming is mutual. This kind of combat in which both tortoises are initially aggressive I call type one combat.

Type one combat occurs in confrontations where neither male is subordinate. Both engage in ramming and biting, and both attempt to overturn each other with their gular projections. Dominance is apparently established when one overturns the other, or when one flees the combat area after a ramming and pushing contest. Evidence of the combat often remains on the ground in the form of a large circular area in which the soil has been tramped by the feet and plastra of the combatants. Similar areas are left after stage two of courtship (Table 2). At the end of type one combat the victorious male holds his head higher than that of the defeated male. If combat ends by one tortoise fleeing, the loser retreats with its head extended directly in front, and the winner pursues with its head inclined about 30° .

Kenneth G. Mentocha and Robert L. Snively, then students at the Bob and Bessie Welder Wildlife Foundation of Sinton, San Patricio County, Texas made field notes on a type one combat they witnessed just southwest of Sinton, Texas. Mentocha wrote:

"24 July, 1965, 6:40 p.m.—2 gopher tortoises in "combat." Heard noise in brush about 20' away. Sounded like a javelina [peccary] moving through the brush. Both tortoises were between a *Xanthoxylum* and a *Celtis pallida*, pushing each other with the gular projections. After about 1 minute they backed off and began to breath heavily as if they had been fighting a long while and were catching their breath. After about 30 seconds they again began the combat. While in close contact, the smaller tortoise continually bit the front portion of the carapace of "Stubby."¹ Stubby seemed to be the stronger of the two and pushed the smaller one around quite a bit. He (Stubby) would put his gular projection beneath the plastron (mostly in the front) and begin to lift the

¹Stubby, the larger of the two tortoises, had no claws but only a large callous on his left front foot.

other in an apparent attempt to turn it over. Three or four times when the smaller tortoise seemed about to be turned over, it placed its forelimbs over and around Stubby's back and seemed to hold on. Stubby pushed the other tortoise backward several times, and usually into a bush where it could not be turned over.

About 7:10 a.m. the two fighters finally came into an open area and Stubby pushed the other tortoise into it. While both had their heads withdrawn and were pushing on one another, I flipped the smaller tortoise onto its back. Stubby then came up to it while it was trying to turn back over and began to bite it on the edge of the shell and the left hind foot. The smaller tortoise turned back over onto its feet and Stubby immediately placed his gular projection under the side of the shell and turned it onto its back again. This time the smaller tortoise lay motionless and Stubby just looked at it for about 30 seconds, then turned around and walked off. The time was about 7:15 a.m. A circle on the ground of about 6' in diameter showed evidence of much scratching, which must have occurred prior to the above observations.

Another kind of combat, type two, occurs between males if only one of the pair is aggressive. In type two combat the aggressive tortoise rams and bites the other one in a series of movements similar to those in stage two of courtship, biting the nonaggressive male on the front feet, head, and the same parts of the shell as on the female during courtship. The nonaggressive male tries to avoid him by pivoting from him in the same circular turning pattern described for the female in courtship. This type of combat ends when the nonaggressive male escapes to a pallet or withdraws all appendages and remains still. While biting is infrequent in type one combat, it is characteristic of type two combat. No dominant males were seen to mount subordinate males.

The following account of type two combat is from my field notes taken at Sinton, Texas, 3 August 1965:

Lake Camp at 10:00: I observed fighting between two males of the 34 tortoises kept in the yard. A large male (male 1) walked rapidly from a clear place on the lawn to a fence 10 feet away where there were three females and a small male (male 2). Male one immediately rammed the smaller male and blocked his access to the females. The male tortoises bobbed their heads when facing one another. Male two was passive at first and his rival turned him completely around twice. Male 2 then bobbed and lunged at the larger tortoise. After a short pause during which both were inactive, male 2 walked toward the center of the lawn away from male 1. Male one followed immediately and bobbed his head in the direction of male 2, exactly as if he were trailing in courtship (Fig. 9A). Male 2 played the female role by nosing items on the ground and slowing his walk. The chase covered about 30 yards and lasted until 10:20, when male 1 overtook male 2 and gently bit the anterior end of his carapace. Male 2 promptly withdrew all appendages. At 10:23 the chase began anew, male 1 trying to overtake male 2 and bite his head. At 10:25

male 2 found and entered a grassy depression and remained there, while male 1 stood behind him and bobbed his head. When male 2 moved, male 1 rammed the exposed rear of his shell. At 10:30 male 1 still stood behind male 2, who remained in the depression; he continued to bob his head in male 2's direction at irregular intervals and then after a short while walked away.

COMBAT IN OTHER *Gopherus*

Less is known of combat than of courtship in other species of *Gopherus*. Woodbury and Hardy (1948), and Grant (1936) report that *agassizi* males charge one another with heads retracted. The contest consists of attempts by one tortoise to overturn the other using the gular projection as both a ram and a lever. Miller (1932) notes that *agassizi* hatchling ram and lunge at each other or at an extended human finger.

Legler and Webb (1961) describe fighting in *flavomarginatus*; I have seen no combat between captives of this species.

Carr (1952) reports on fights between males and females of *G. polyphemus*. I have seen ramming between a captive male and female of this species, but it was not clear if these contests were part of courtship or combat. I saw one particularly ambitious, moderate-sized, malformed, male *polyphemus* repeatedly ram a subadult *Geochelone elephantopus* and an adult *G. pardalis*, both of which were at least 20 pounds heavier than the militant *polyphemus*. I gained some information on *polyphemus* combat by watching confrontations between males in the laboratory.

In these experiments each of six adult male tortoises was marked and kept in a rectangular indoor pen. The room housing the pens was kept on a 9½-hour day throughout the experimental period (1 February-1 April 1965). Air temperature for the entire test period varied from 76° F. to 78° F.

For each trial two tortoises were placed diagonally from each other in one of the rectangular pens. Prior to each trial I sprinkled the tortoises with water, which seemed to stimulate them. In the field I have noted that tortoises are often more active after rain. Watching from the concealment of a blind made no observable change in the tortoise behavior and so was discontinued. I recorded the distances between tortoises when head bobbing first occurred. Each trial lasted until the tortoises failed to react to each other. Portions of the trials were recorded on 180 feet of motion picture film. The analysis of these interactions including the filmed portions follows.

The responses between two male *polyphemus* consist of initial responses, locomotion, head bobbing, mutual smelling, and establish-

ment of a dominant-subordinate relationship. I considered a tortoise highly motivated if it reacted immediately to the presence of another tortoise at the start of the trial, and poorly motivated if its reactions were delayed longer than 2 or 3 minutes. I used the word contact to define the moment when the tortoises touched one another following directed (see below) locomotion by one or both of the reptiles.

INITIAL RESPONSES.—When an intruder was placed in their pens tortoises either remained still, immediately proceeded toward the intruder, or in a few cases turned into a corner. Poorly motivated individuals spent 3 to 4 minutes smelling the substrate of the pen or old feces before actually pointing their head in the direction of the other animal. Highly motivated tortoises began to walk immediately in the other reptile's direction.

LOCOMOTION.—I define locomotion as directed if influenced by another tortoise, and nondirected if apparently not influenced by the other tortoise. In directed locomotion a highly motivated tortoise walks rapidly with his neck fully extended. In nondirected locomotion the pace is slower and the neck is only partially extended.

HEAD BOBBING.—Eglis (1962) classed head bobbing in *Gopherus* as "dirolent". Bobbing usually occurs first when the tortoises are about 2½ feet apart.

The function of head bobbing in *polyphemus* is not clear. The fact that a tortoise's head is always pointed in the direction of another tortoise when bobbing occurs suggests that a visual cue may be involved, but a highly motivated tortoise will walk toward another tortoise in the absence of reciprocal bobbing or reciprocal directed locomotion. Continued bobbing or directed locomotion by a poorly motivated tortoise is dependent on reciprocal head bobbing or directed locomotion by the other animal.

As the behavioral functions of head bobbing are largely unknown, anthropomorphic adjectives such as "contentment," "enthusiastic," and "nod of friendship" used in conjunction with head bobbing can serve only to confuse otherwise informative reports (Nichols, 1953).

MUTUAL SNIFFING.—At contact the vertical bobs of both tortoises assume a large lateral component and finally lose any recognizable pattern. The head and feet of both tortoises are the objects of sniffing. The vertical bobs associated with these sniffing movements are often interrupted by a lateral wiping motion directed to the surface of one of the forelegs. After 1 to 2 minutes of mutual sniffing, one of the tortoises becomes more active than the other.

DOMINANCE-SUBORDINANCE.—Tortoises demonstrate dominance re-

relationships clearly by their postures. The dominant tortoise supports its weight on all four of its extended legs. He may walk around the other tortoise, stopping often to smell his rear legs. The submissive tortoise holds his head low and his neck only partially extended. If the dominant tortoise continues to investigate, the submissive tortoise positions himself at an angle of approximately 45° to the dominant tortoise and maneuvers to keep one side or the other always presented to the front of the dominant individual. This he does by pivoting on the anterior portion of his plastron with his rear legs, keeping the front legs withdrawn. After 1 or 2 minutes of this behavior the more active dominant individual will turn away, apparently no longer interested in the other tortoise. Dominance can be demonstrated by placing food in a pen with two tortoises; a dominant tortoise inhibits feeding by a subordinate tortoise.

The males of several tortoise and turtle species engage in shell ramming during combat and to immobilize the female prior to copulation (Nikolskii, 1915; Taylor, 1933; Brumwel, 1940; Hamilton, 1944; Auffenberg, 1964b). While I observed no ramming in these tests, I did see ramming in the following spring and summer between males of *polyphemus*, and *polyphemus* male ramming males of both *Geochelone elephantopus* and *G. pardalis*.

The presence of a distinct dominant-submissive relationship in *Gopherus* suggests that such behavior may be species-specific. It is conceivable that in meetings between *polyphemus* males (or females in the non-breeding season), noncombative recognition of dominance would result in the subordinate tortoise leaving the dominant individual's presence. These particular experiments failed to show that a given *polyphemus* is dominant to any intruder introduced into its "home" pen. Instead certain individuals tended markedly to be dominant both in their own pens and in those of other tortoises.

BEHAVIORAL ELEMENTS COMMON TO COURTSHIP AND COMBAT

In tortoise courtship and combat one member of the pair becomes the aggressor. In courtship it is usually the male. Courtship ends when the female is immobilized for intromission. In *G. berlandieri* agonistic behavior continues in type one combat until one tortoise is overturned or pushed away, and in type two combat until the non-aggressive member of the pair escapes by fleeing or retreating to a shelter. In some instances a dominance relationship may be established without fighting, as shown by the experiments using male *G.*

polyphemus. In *berlandieri* dominance is established by behavior patterns common to both courtship and combat, particularly type two combat. This behavior includes head position, shell ramming, and biting.

When two *berlandieri* males approach one another, or when a male approaches a nonaggressive male, their respective head positions show whether the confrontation will be type one or type two combat. An aggressive tortoise holds his head higher and extends it farther outward than a nonaggressive tortoise. The subsequent behavior of the nonaggressive male or female is often seemingly unrelated to either combat or courtship.

In meetings between two aggressive tortoises both hold their heads high, and each reacts aggressively. During the ramming and biting in stage two of courtship the male tortoise's head is held higher than that of the female, who finally retracts her head partially or fully just prior to and during presentation.

Shell ramming in courtship results in immobilization of the female. In *berlandieri* males the shell ramming of type one combat ultimately determines dominance. The ramming movement in type one combat has an upward arc at the end of the forward thrust to overturn the other tortoise. The upward arc is absent in courtship and type two combat ramming of *berlandieri*.

In *berlandieri* type two combat all four legs of the dominant male are extended and his head is nearly fully extended and arched. The subordinate male withdraws his feet and fully or partially withdraws his head, which is thus lower than that of the dominant male. Similarly in courtship the female finally withdraws her head and front feet, but leaves her rear feet extended. Both the subordinate male in type two combat and the subordinate female in courtship support at least part of their weight on the plastron, while the dominant male stands on all four legs.

EXPERIMENTS

The preceding observations were based on field work. To evaluate the field work more clearly laboratory experiments were designed to find the cues *berlandieri* uses to distinguish sex in its own species. I used nonparametric statistics for analysis because I doubt that the data conform to all the assumptions underlying the appropriate parametric tests, particularly the interval measurement scale. With this in mind I used the Kruskal-Wallis one-way analysis of variance, and in one case the Chi-square test, to determine the homogeneity of

groups of data, and the Fisher-Exact Probability test to compare medians within groups of data.

OPEN SQUARE TESTS

With these experiments I hoped to detect a differential investigative response by male and female tortoises to other male and female tortoises and controls. I put the test tortoise in the large open square box and used individual male and female tortoises in the small removable cage as stimuli. The empty removable cage served as a control.

The tortoises were tested when the chin glands were active (Fig. 11) (21 July 1966; 5 November 1966) and inactive (11 April 1967; 1 June 1967). The data for tortoises with active chin glands came from 22 different males and 15 different females used for a total of 41 trials, each lasting 24 hours.

Responses for tortoises with inactive glands (Fig. 12) were gathered from 15 different males and females for a total of 30 trials lasting 24 hours each. The trials were distributed equally between two open square testing boxes. The analysis of these scores provides the following results:

(1) When the chin glands were active, males had a poor ability to differentiate between males, females, and controls ($p \leq 0.15$); their ability to distinguish females from controls or other males was not significant, but they tended to respond more to other tortoises (males and females collectively) than to controls ($p = 0.20$).

(2) Females with active glands easily differentiated males from controls or other females ($p \leq 0.05$).

(3) Males with inactive chin glands did not respond equally to the three stimuli ($p \leq 0.05$), but favored other males over females or controls ($p = 0.10$).

(4) Females showed no differential response when their chin glands were inactive.

(5) Males and females responded more to all stimuli when their glands were active than when they were inactive ($p \leq 0.01$).

CLOSED SQUARE TESTS

RESPONSE TO LIVE ANIMALS.—I used live animals as stimuli to test if tortoises could distinguish sex on the basis of movements and external morphology. Five different males and females were used for a total of 15 trials. The tortoises used as stimuli were confined in a

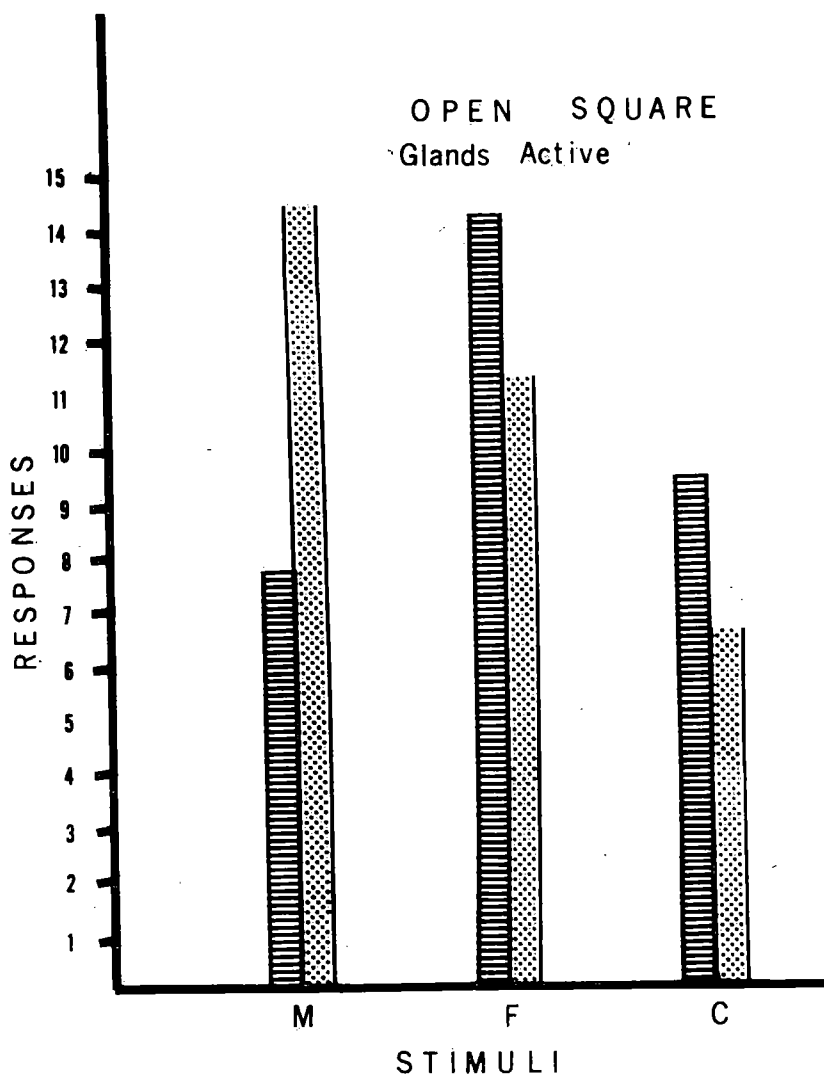


FIGURE 11. Results of open square tests. The vertical scale represents the average ranked scores used in the Kruskal-Wallis analysis of variance. Barred columns are male responses, dotted columns female responses. Stimuli used to elicit responses are M, male *G. berlandieri*, F, female *G. berlandieri*, C, controls.

sealed glass aquarium which was placed into the small, removable cage (Fig. 3). Thus a response by the test animal would have to be based on something other than olfactory cues. Controls were the

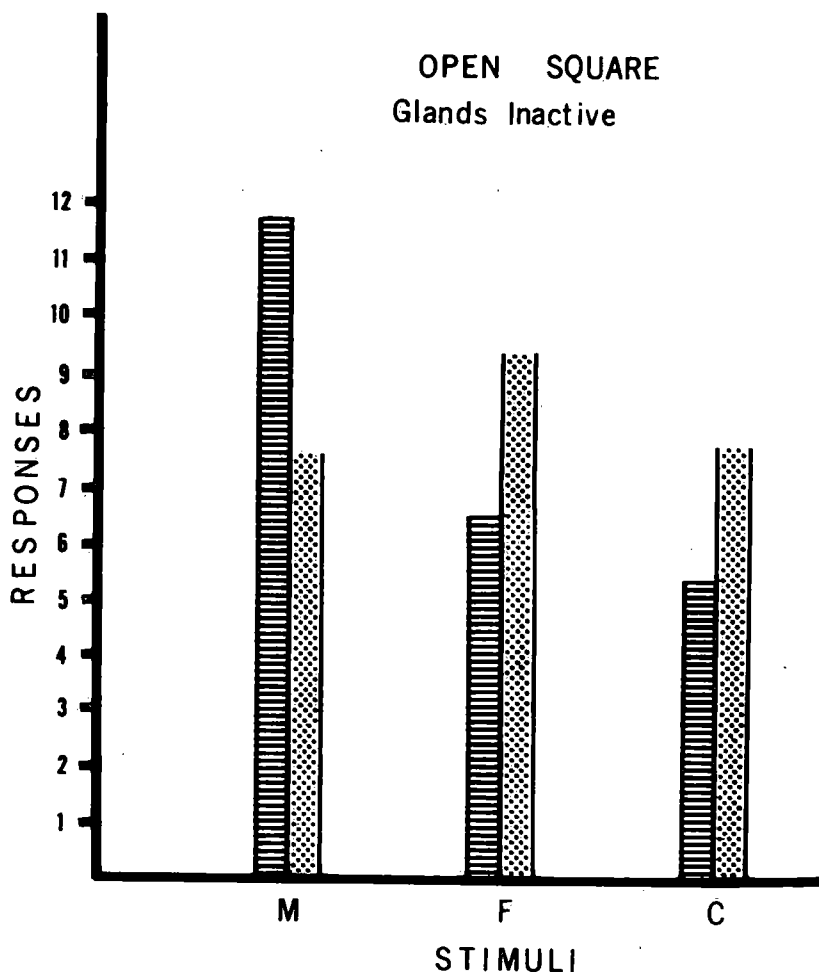


FIGURE 12. Results of open square tests. See legend for figure 11.

empty aquarium in the removable cage. The tortoises were tested (July 1967) when their chin glands were secreting. As the open square experiments showed that 90 per cent of the responses recorded during a trial were made during the first 4 hours, each trial lasted 4 hours.

RESPONSE TO PRESERVED TEST ANIMALS.—I used formalin preserved tortoises as stimuli to test the ability of tortoises to distinguish sex by visual cues in the closed square experiments. The sealed aquarium eliminated olfactory cues and the life-like stances removed the chance

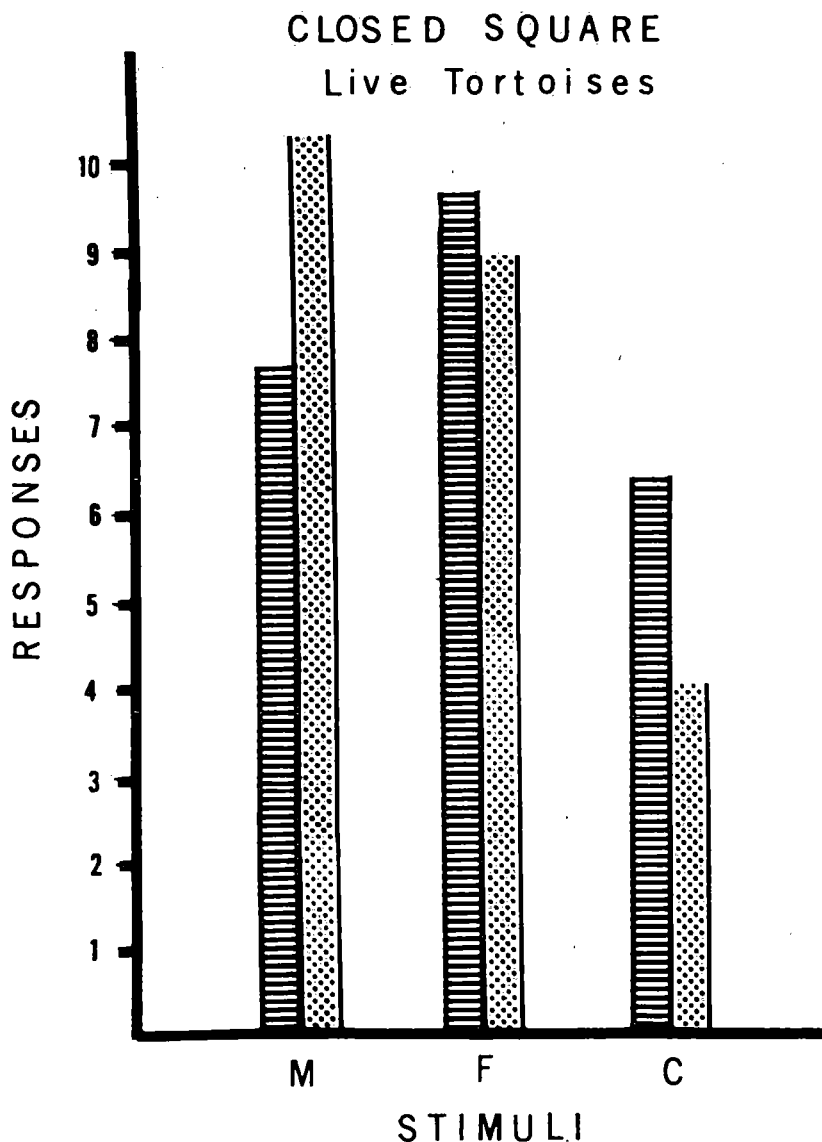


FIGURE 13. Results of closed square tests. See legend for figure 11.

that a sex or species-specific movement were possible cues. This experiment therefore tested the role of external morphology in sexual discrimination. The tortoises were tested when their chin glands were active (July and August 1967). Each trial lasted 4 hours and

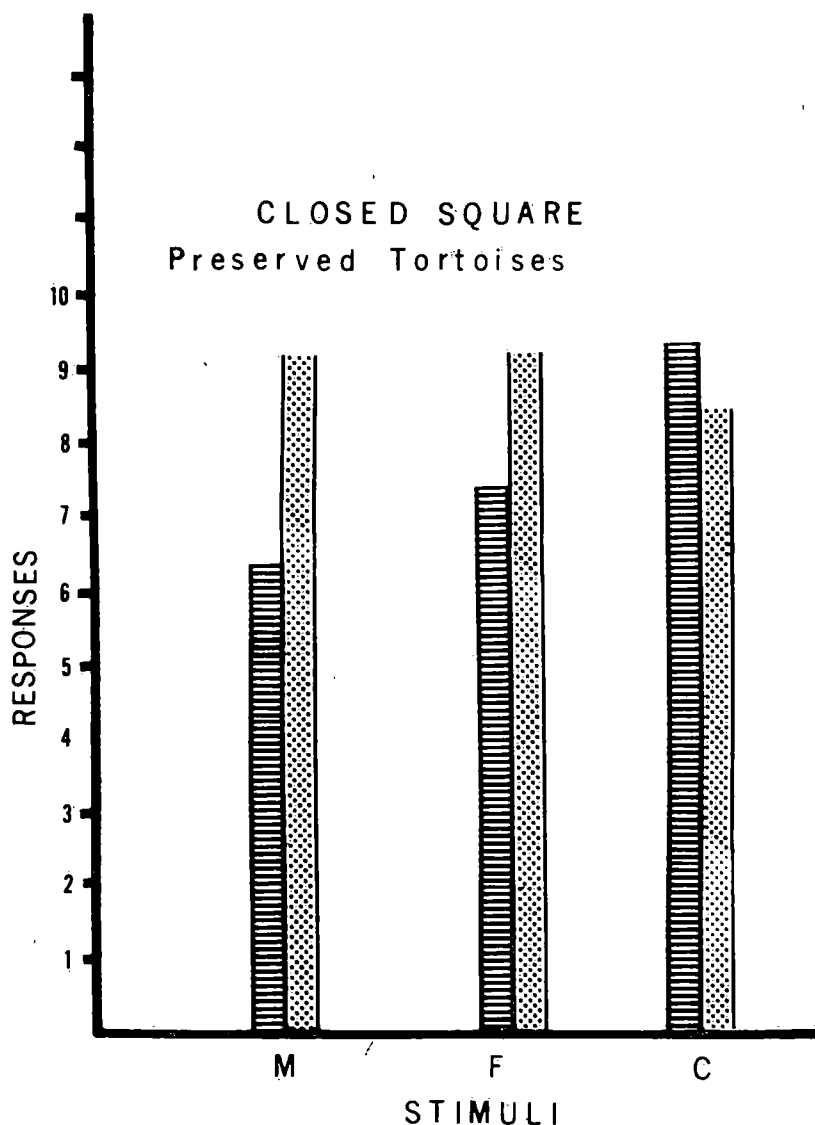


FIGURE 14. Results of closed square tests. See legend for figure 11.

the controls were empty aquaria. The test tortoises again consisted of five different males and females used for a total of 15 trials.

(1) The males showed no significant ability to differentiate between males, females, and controls when movement (Fig. 13) or external morphology (Fig. 14) were the stimuli.

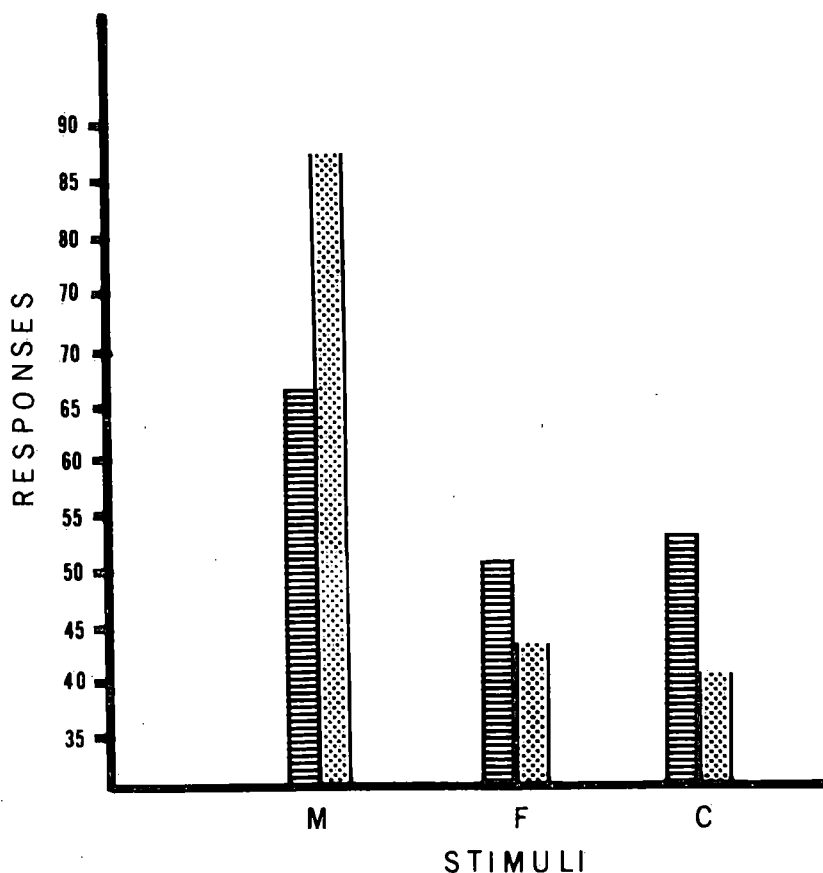


FIGURE 15. Response to cloaca scent. See legend for figure 11.

(2) Females tended to react more ($p \leq 0.15$) to moving tortoises (Fig. 13) than to controls, but made no significant differential responses on the basis of external morphology alone (Fig. 14).

CLOACA SCENT TESTS

I evaluated the ability of tortoises to distinguish sex on the basis of cloaca odor by comparing their responses to cotton swabs smeared with cloacal material from each sex (Fig. 15). Controls were clean cotton swabs. Jar positions were switched so that male, female, and control swabs appeared an equal number of times at each station. The jars were washed after each trial. The tests were performed

from 15 October 1966 through 10 November 1966. Each trial lasted 24 hours. A total of 20 females and 22 males were used.

Male *Gopherus berlandieri* were unable to distinguish between male, female, and control swabs. The females did not respond equally to all three test items ($p \leq 0.02$) but responded more to the cloaca scent of males than of females ($p = 0.025$).

HORMONE INJECTIONS

I used subcutaneous hormone injections to observe possible effects of hormones on behavior and chin gland activity. On 11 March 1967 I selected three pairs of healthy male tortoises of approximately equal size and injected one member of each pair with 20 mg of testosterone phenylacetate. I estimated dosage from Evan's (1951) work on *Chrysemys* (then *Pseudemys*) *scripta troosti* on the basis of carapace length. One pair remained in an outdoor pen, another was put in an indoor pen on a 24-hour day, and the third pair put in an indoor pen on a 5-hour day. By 14 March the chin glands of the experimental tortoises on the 5-hour day were enlarged and secreting. The glands of the experimental tortoises in the outdoor pen produced some secretion and were slightly enlarged. The glands of the experimental tortoises on the 24-hour day and those of all the controls produced neither a secretion nor become enlarged. In the outdoor pen two males injected with testosterone initiated some pushing not clearly definable as type one or type two combat with some of the noninjected tortoises.

These observations indicate that in male tortoises the chin gland's activity is influenced by the concentration of the male sex hormone and changes in day length.

Injections of 25 mg of progesterone in adult females and 20 mg of testosterone in adult males when the glands of both sexes were active (July 1967) made no observable change in the condition of their chin glands or behavior. Injections of 50 mg of thyroxine in males and females seemed to stimulate appetite.

Investigative behavior consisting of partial head bobs can be elicited from males and females by placing small amounts of testosterone phenylacetate or progesterone in front of the tortoise's nose. Francis Rose (pers. comm.) reported a spray emanating from the chin glands of a male *G. berlandieri* copulating with a female.

DISCUSSION

Successful mating behavior depends on sexual discrimination. *G. berlandieri* accomplishes sexual discrimination during four stages of

courtship (Table 2). Several tortoise species are sympatric and individuals of closely related sympatric populations often segregate themselves by species-specific mating behavior. In such sympatric populations courtship is more complex by the additional problem of species identification.

Courtship in *berlandieri* (Table 2) differs in two major respects from that of *polyphemus* (Table 3): the initiation of courtship by the female in *polyphemus* and the regions of the female's shell bitten by the male. Females of *polyphemus* may initiate courtship by approaching males; this I have never observed in *berlandieri*, but the *berlandieri* female does play a subtle and not impassive role in courtship. Laboratory tests (Fig. 11) show that *berlandieri* females are more responsive to males than to females during the breeding season (approximately that period when the chin glands are actively secreting), and it is they and not the males that can distinguish sex by cloaca scent alone (Fig. 15).

Differences in the behavior of *berlandieri* and *polyphemus* may explain the relative aggressiveness of the respective females during courtship. Courtship observations of *G. polyphemus* are based on tortoises from typical populations where individuals construct burrows and maintain more or less well-defined territories (Auffenberg 1966a). Individuals of these populations occupy more or less mutually exclusive areas where contact with other tortoises is restricted. Thus individual males and females must leave their own activity area to search for other tortoises during the breeding season. Bastock (1967) postulates an active response by females to threat and courtship displays of males as an evolutionary result of territorial behavior. The courtship of *berlandieri* was based mainly on individuals from nomadic populations of the Jackass Prairie near Brownsville, Texas where both sexes often meet in their daily movements (Auffenberg and Weaver, 1969). The ability of the female *berlandieri* to detect males by confrontations (Fig. 11), cloacal scent (Fig. 15), and her tendency to be attracted to moving tortoises of either sex (Fig. 13), ensure her discovery by males during the breeding season. Thus initial meetings of potential breeding pairs are due to (1) a biased attraction of females for moving tortoise-like objects and (2) a probable high but random investigative behavior of males.

The males of both *polyphemus* and *berlandieri* consistently bite different areas of the female's shell during courtship. Male *berlandieri* bite the female's head, front legs, and, most consistently, the upper part of the female's carapace in the region of the nuchal bone.

This biting becomes increasingly forceful during courtship. Courtship biting by *polyphemus* males is concentrated on the female's gular projection and is less forceful. I interpret the selection of such specific biting targets to be a highly specific behavior of considerable importance in the courtship of the two species. The courtship of the two species groups is mutually exclusive, possibly because of isolating mechanisms resulting from Pleistocene sympatry (Fig. 1). This conclusion is supported by hybridization between species of one group (the *agassizi* group) that produced living offspring (Householder, 1950; Woodbury, 1952) and a notable absence of any intergroup courtship when members of both species groups were present together during the breeding season. On these occasions I put males and females of *berlandieri*, *agassizi* and *polyphemus* in indoor and outdoor pens, but observed courtship only between males and females of the same species, or between members of the *agassizi* group (*agassizi* and *berlandieri*).

The field and laboratory observations show that *berlandieri* consistently makes heterosexual preferences only when its chin glands are secreting. Analysis shows the glands' secretion contain aromatic compounds differing in composition and concentration in males and females (Rose, *et al.*, 1969). In males this gland secretion is probably controlled in part by testosterone level and day length.

Sexual discrimination in *berlandieri* is accomplished differently by each sex. The female can distinguish males from females by cloacal scent, but the chemical or visual cues the male uses are not known. My experiments show that males cannot recognize females by cloacal scent, external morphology, or movement, which suggests that sexual discrimination by males may rest in part with the chemical differences of the chin gland secretion. This interpretation is suggested by the difference in the male's response to the open square experiments when his chin glands are active and inactive (Fig. 11). Males respond to females when chin glands are active in both sexes, and to males when the glands are inactive in both sexes. Females react to males when the glands of both sexes are active, but do not discriminate when glands are inactive. The female's ability to detect the male by cloaca scent (and perhaps by feces also), and her positive response to moving tortoise-like objects orient her toward the male. A stage resembling trailing (Table 2, Stage 1) occurs in type two combat between males. Sexual identification by the male probably occurs in stage two when close contact occurs. Intromission is accomplished only if the female cooperates by presenting, a behavior

not seen in type two combat between males, and by partially extruding her cloaca toward that of the mounted male. If a female fails to identify another tortoise as a male by cloacal scent, she will not present and thus prevent intromission. I have never seen male *berlandieri* present or mount other males in combat. In stage two of courtship the female presents and mounting occurs. I interpret this to mean that presentation by females releases mounting and copulatory behavior in males and therefore sexual discrimination by males is partly dependent on a behavioral cue. Both a sexually-specific chin gland secretion and a sexually-specific behavior by the female enables the male to distinguish sex.

The open square experiments show that males respond more to males than to females when chin glands are inactive (Fig. 12). This is confirmed by the following field observations: (1) I have seen combat but not courtship behavior by adult males when the glands were inactive; (2) combat frequently occurs among juveniles when the glands are presumably inoperative (at least no reaction is observable and the glands are not seasonally enlarged); (3) most of the combat observations are from early in the reproductive season when the glands were not active or had not reached their greatest activity (the chin glands of individuals in the Brownsville populations were not enlarged until late June or early July). I have never seen females ram or otherwise behave aggressively toward males, therefore type one combat occurs only between males. If a tortoise assumes a subordinate role in a confrontation with another tortoise, it may be a nonaggressive adult male, an adult female, or a juvenile of either sex. The subsequent behavior will be either courtship or type two combat.

Head movements are known to be visual signals in *Geochelone carbonaria* and *G. denticulata* (Auffenberg, 1965). I do not believe that a visual sex or species-specific signal is the primary role of head bobbing in *G. berlandieri*. It is most frequently performed by the male during the trailing stage of courtship when he is out of the female's visual field. Males often bob at females in pallets and also when the male is out of the female's visual field. Males may scarcely bob at all, or erratically, when confronting a female. These observations lead me to conclude that head bobbing in *berlandieri*, and probably in the other *Gopherus* species, is primarily a sniffing movement. Head bobbing does have species-specific differences in *Gopherus* (Fig. 8), but no known visual discriminatory function as in *Geochelone carbonaria* and *G. denticulata*.

In *Gopherus* head bobbing may be in an early stage of emancipation to a visual signal function from a movement attending olfaction. This conclusion is supported by such observations as those made on a male captive *agassizi* who bobbed at a female *berlandieri* only when she turned her head into his field of vision. Bobbing in all species of *Gopherus* may not have exactly the same role, some species being more specialized than others with respect to head bobbing as a visual signal. The type of head movements performed by the South American *Geochelone* in species discrimination are the same as those they use in olfaction. Head movements as visual signals in *Geochelone* are derived directly from the head movements associated with olfaction.

In some species of *Gopherus* head bobbing may be an insignificant visual signal, but in *berlandieri* and *polyphemus* the angle a male tortoise inclines his head serves as a visual status indicator to other tortoises. Dominant males incline their heads at a higher angle than subordinate males. In courtship the neck of an aroused courting male *G. berlandieri* is fully outstretched and inclined in a high arch. A male thus sexually aroused automatically exhibits a display of dominance and inhibits interruptions by other less motivated males.

The question of dominance is central to courtship or combat. The similarity of behavior used to establish dominance in both courtship and combat in *berlandieri* suggests that the behavioral units of courtship are derived from those of combat. While neither *berlandieri* nor *polyphemus* court species of other genera in captive situations, I have seen *berlandieri* males and both sexes of *polyphemus* ram individuals of other species of *Gopherus* and individuals of species of other genera. *G. agassizi* hatchlings ram one another (Miller, 1932), and I have seen young *polyphemus* up to a year of age do the same. I have never seen yearlings of *Gopherus* species attempt to copulate. Combative behavior in adults arises from many situations, such as limited food, space, or shelter. Species-specific courtship behavior evolves in tortoises only when sympatry with other turtle or tortoise species confuses species identification. Tortoise species with a long history of allopatry are notorious for their lack of species discrimination during the breeding season. Footballs, rocks, or any tortoise-resembling object appeal equally to the nondiscriminating male tortoise. Courtship is a block of behavioral elements apparently emancipated from phylogenetically older combat, specifically in *berlandieri*, from type two combat.

Displacement activity is abundantly reported for many groups of

animals. Basically it consists of a behavior that is ritualized and emancipated from one set of casual factors to another. (Tinbergen, 1952; Blest, 1963). Displacement activity often consists of comfort movements that appear to arise in the presence of intense conflicting drives (Hess, 1965). The behavior of female tortoises in the trailing stage of courtship (Table 2, Stage 1) or of nonaggressive males in the early stages of type two combat appears to be displacement activity.

LITERATURE CITED

- Agassiz, A. 1857. Contributions to the natural history of the United States of America, vol. 1. Boston: Little Brown and Co. Pp. 235-452.
- Auffenberg, W. 1964a. A redefinition of the fossil tortoise genus *Stylemys* Leidy. J. Paleontol. 38: 316-324.
- . 1964b. Notes on the courtship of the land tortoise *Geochelone travancorica* (Boulenger). J. Bombay Nat. Hist. Soc. 61: 247-253.
- . 1965. Sex and species discrimination in two sympatric South American tortoises. Copeia, 1965: 335-342.
- . 1966a. On the courtship of *Gopherus polyphemus*. Herpetologica. 22: 113-117.
- . 1966b. The carpus of land tortoises (Testudininae). Bull. Florida State Mus. 10: 159-191.
- . Tortoise behavior and survival. BSCS Pamphlet Series. Pp. 5-38.
- and W. G. Weaver, Jr. 1969. *Gopherus berlandieri* in southeastern Texas. Bull. Florida State Mus. 13(3): 141-203.
- Bastock, Margaret. 1967. Courtship: an ethological study. Illinois: Aldine Publishing Co. Pp. 1-220.
- Beltz, R. E. 1954. Miscellaneous observation on captive Testudininae. Herpetologica. 10: 45-47.
- Blest, A. D. 1963. The concept of ritualization, pp. 102-124, in Current problems in animal behavior. W. H. Thorpe and O. L. Zanolli, eds., England, Cambridge Univ. Press.
- Brumwell, M. J. 1940. Notes on courtship of the turtle, *Terrapene ornata*. Trans. Kansas Acad. Sci. 43: 391-392.
- Camp, C. L. 1916. Notes on the local distribution and habits of amphibians and reptiles of southeastern California in the vicinity of the Turtle Mountains. Univ. Calif. Publ. Zool. 12: 503-544.
- Campbell, Howard W. and William E. Evans. 1967. Sound production in two species of tortoises. Herpetologica. 23: 204-209.
- Carpenter, C. R. 1962. Societies of monkeys and apes, pp. 24-51, in Primate social behavior, Charles H. Southwick, ed., Princeton, D. Van Nostrand Company, Inc.
- Carr, Archie. 1952. Handbook of turtles. New York: Comstock Publication.
- DeSola, R. 1930. The Liebespiel of *Testudo vandenburghi* a new name for the mid-Albemarle Island Galapagos tortoise. Copeia, 1930: 79-80.

- Ditmars, R. L. 1910. Reptiles of the world. New York: Sturgis Walton Company.
- Doumerque, F. 1899. Essai sur la Faune erpetologique de l'Oranie. Soc. Geogr. Arch. Oran. 19: 197-260, 501-502.
- Eglis, A. 1962. Tortoise behavior: a taxonomic adjunct. Herpetologica. 18: 1-8.
- 1963. Nesting of a parrot-beaked tortoise. Herpetologica. 19: 66-68.
- Evans, L. T. 1951. Effects of male hormone upon the tail of the slider turtle *Pseudemys scripta troostii*. Science. 114: 277-279.
- FitzSimons, V. 1935. Notes on a collection of reptiles and amphibians made in the southern Kalahari, Buskmanland and Great and Little Namagua land. Ann. Transvaal Mus. 15: 519-550.
- Grant, Chapman. 1936. The southwestern desert tortoise, *Gopherus agassizii*. Zoologica. 21: 225-229.
- 1946. Data and field notes on the desert tortoise (*Gopherus agassizii*). Trans. San Diego Soc. Nat. Hist. 10: 399-402.
- 1960. Differentiation of the southwestern tortoises (genus *Gopherus*) with notes on their habits. Trans. San Diego Soc. Nat. Hist. 12: 441-448.
- , and C. R. DeSola. 1934. Antillean tortoises and terrapins: distribution, status and habits of *Testudo* and *Pseudemys*. Copeia, 1934: 73-79.
- Hamilton, Rodgers D. 1944. Notes on the mating and migration of berlandiers turtle. Copeia, 1942: 62.
- Hay, Oliver P. 1908. The fossil turtles of North America. Carnegie Inst. Washington, Spec. Publ. 75: 1-268.
- Heller, Edmund. 1903. Papers from the Hopkins Stanford Galapagos Expedition 1898-99, XVI. Reptilia. Proc. Washington Acad. Sci. 5: 39-98.
- Hess, E. H. 1965. Ethology: an approach toward the complete analysis of behavior, in Readings in animal behavior. Holt, Rinehart and Winston.
- Householder, V. H. 1950. Courtship and coition of the desert tortoise. Herpetologica, 6: 11.
- Legler, J. M. and R. C. Webb. 1961. Remarks on a collection of Bolson tortoises, *Gopherus flavomarginatus*. Herpetologica, 17: 26-37.
- Miller, L. 1932. Notes on the desert tortoise (*Testudo agassizii*). Trans. San Diego Soc. Nat. Hist. 7: 187-208.
- Mykytowycz, R. 1965. Further observations on the territorial functions and histology of the submandibular (chin) cutaneous glands in the rabbit. Anim. Behav. 13: 440-412.
- Nichols, Una G. 1953. Habits of the desert tortoise, *Gopherus agassizii*. Herpetologica, 9: 65-69.
- 1957. The desert tortoise in captivity. Herpetologica, 13: 141-144.
- Nikolskii, A. M. 1915. Fauna of Russia and adjacent countries, vol. 1, Reptiles. Zool. Mus. Russ. Cad. Sci. pp. 1-532.
- Rose, Francis L., Robert Drotman, and William G. Weaver. 1969. Electrophoresis of chin gland extracts of *Gopherus* (Tortoises). Comp. Biochem. Physiol. 29: 847-851.

- Rose, Walter. 1950. The reptiles and amphibians of Southern Africa. M. Miller, Capetown, pp. 1-378.
- Siegel, Sidney. 1956. Nonparametric statistics for the behavioral sciences. New York: McGraw-Hill.
- Smith, H. and S. D. Brown. 1946. A hitherto neglected integumentary gland in the Texan tortoise. Proc. Texas Acad. Sci. 30: 45.
- Snedigar, R. and Rokosky, E. J. 1950. Courtship and egg laying of captive *Testudo denticulata*. Copeia, 1950: 46-48.
- Taylor, E. H. 1933. Observations on the courtship of turtles. Univ. Kansas Sci. Bull., 21: 269-271.
- Tinbergen, N. 1952. Derived activities; their causation, biological significance, origin and emancipation during evolution. Quart. Rev. Biol., 27: 32.
- Van Denburgh, J. 1914. The gigantic land tortoises of the Galapagos archipelago. Proc. California Acad. Sci. 2: 203-374.
- Watson, George E. 1962. Notes on copulation and distribution of Aegean land tortoises. Copeia, 1962: 317-321.
- Wermuth, H. and R. Mertens. 1961. Schildkroten, Krokodile, Bruckenechsen. Veb Gustav Fischer Verlag, Jena.
- Woodbury, A. M. 1952. Hybrids of *Gopherus berlandieri* and *G. agassizii*. Herpetologica, 8: 33-36.
- and Hardy R. 1948. Studies of the desert tortoise *Gopherus agassizii*. Ecol. Monogr. 18: 145-200.

Contributions to the BULLETIN OF THE FLORIDA STATE MUSEUM may be in any field of biology. Manuscripts dealing with natural history or systematic problems involving the southeastern United States or the Caribbean area are solicited especially.

Manuscripts should be of medium length—50 to 200 pages. Examination for suitability is made by an Editorial Board.

The BULLETIN is distributed worldwide through institutional subscriptions and exchanges only. It is considered the responsibility of the author to distribute his paper to all interested individuals. To aid in this, fifty copies are furnished the author without cost.

PREPARATION OF MANUSCRIPT

Highly recommended as a guide is the volume:

Conference of Biological Editors, Committee on Form and Style.
1964. Style manual for biological journals. (Second Edition)
Amer. Inst. Biol. Sci., Washington. 117 pp.

Manuscripts should be typewritten with double spacing throughout, with ample margins, and on only one side of the paper. The author should keep a copy; the original and a carbon must be submitted. Tables and legends of figures should be typed on sheets separate from the text. Several legends or tables may be placed on a single sheet.

Illustrations, including maps and photographs, should be referred to as "figures." All illustrations are reduced to a maximum of 4-1/4 by 7-1/8 inches. Size scales, wherever they are necessary, should be incorporated into the figure.

References to literature should conform with the bibliographic style used in recent numbers of the BULLETIN. Spell out in full the titles of non-English serials and places of publication.

Footnote material should be kept to a minimum. However, provide copy for a footnote detailing the title, affiliations, and address of the author (see recent numbers of the BULLETIN).

Manuscripts must be accompanied by a synopsis—a brief and factual summary (not a mere description) of the contents and conclusions, which points out the presence of any new information and indicates its relevance. In it list all new organisms described and give their ranges; indicate all taxonomic changes proposed. The synopsis, written in full sentences, should be concise, but completely intelligible in itself without references to the paper, thereby enabling the busy reader to decide more surely than he can from the title alone whether the paper merits his reading. The synopsis will be published with the paper. It does not replace the usual conclusions or summary sections. It may also serve as copy for the abstracting services.

Manuscripts and all editorial matters should be addressed to:

Managing Editor of the BULLETIN
Florida State Museum
Seagle Building
Gainesville, Florida