Analysis of courtship behaviors of the desert tortoise, Gopherus agassizii

Rebecca Lynn Holte

University of Nevada, Las Vegas

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ANALYSIS OF COURTSHIP BEHAVIORS OF THE DESERT TORTOISE.

GOPHERUS AGASSIZII

by

Rebecca Lynn Holte

Bachelor of Arts in Biology
Gustavus Adolphus College, St. Peter, Minnesota
1995

A thesis submitted in partial fulfillment
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Examination Committee Member

Graduate College Faculty Representative
ABSTRACT

Analysis of courtship behaviors of the desert tortoise, *Gopherus agassizii*

by

Rebecca Lynn Holte

Dr. Charles Douglas, Examination Committee Chair
Adjunct Professor of Biological Sciences
University of Nevada, Las Vegas

General descriptions of courtship behavior have been published for the desert tortoise, *Gopherus agassizii*. However, the amount and sources of variation in courtship behaviors have not been documented. I examined courtship behavior by analyzing videotaped interactions between captive males and females. I calculated duration of three courtship phases (trailing, subduing, and mounting) and quantified the number and rate of rams and bites. Male courtship behavior changed with increased courtship experience, and smaller males showed more variable behavior than larger males. Larger males bit small females at higher rates than did smaller males. Courtship varied in response to female size. Large males bit smaller females at faster rates than they bit larger females, an indication of behavioral plasticity. Males in successful matings were larger, mounted longer, rammed less, and bit more than males in unsuccessful matings. These results lend insight into the sources and amount of variability in reptilian reproductive behaviors.
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CHAPTER 1

INTRODUCTION

Since the Mojave population of the desert tortoise, *Gopherus* [=*Xerobates*; Bour and Dubois 1984] *agassizii*, was declared threatened under the Endangered Species Act on April 2, 1990, it has become increasingly important to learn as much as possible about the behaviors of this species. Variation in courtship behaviors of male *G. agassizii* has not previously been quantified; the intent of this study was to gain insight into the amount and sources of variability in reptilian courtship behaviors using the desert tortoise.

Variation in behavior

Variation in behaviors can be caused by numerous factors. Genetic variation, ontogeny, behavioral plasticity, learning, and environmental variation can each potentially play a role in behavioral variability. Variation can be found at large scales within a species, as with Australian zebra finches (*Taeniopygia guttata castanotis*), which exhibit large-scale geographic variation in their calls (Zann 1993). The number of syllables in calling songs of the male bushcricket (*Ephippiger ephippiger*) calling song

1

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varies along a geographical cline (Ritchie 1992). Variation can also occur at smaller scales, within an individual. Grey treefrogs, *Hyla versicolor*, have both between-male variation and within-male variation in their mating calls (Gerhardt 1991). Male green iguanas, *Iguana iguana*, show appreciable amounts of variation in some types of head bobs, while there is very little variation in other types of head bobs (Dugan 1982). Many such examples of intraspecific variation in reproductive behaviors can be found within the kingdom Animalia. Variation in male courtship behaviors may affect reproductive success, particularly if females choose from different qualities in males.

Mate choice behavior can have genetic components, as found in wild house mice. *Mus domesticus* (Lenington et al. 1992). A group of genes related to mating preference influences which male genotype the females prefer. Bakker (1993) found that the coloration of male three-spined sticklebacks, *Gasterosteus aculeatus*, exhibited genetic variation and that female preference for brighter coloration was genetically determined. Animals with different genotypes and behaviors are then a potential source of variation in mate choice behaviors.

Behavioral plasticity is the capacity of an organism to vary its behavior as a reaction to environmental conditions (Lincoln et al. 1985). The ability to change behavior to adjust to a set of circumstances may be adaptive in that it could maximize the chances of an organism to reproduce or leave offspring (Wilson 1975). In courtship, behavioral plasticity could offer advantages to males, for instance, where a novel change in a male's courting behavior elicits the attention of a previously uninterested female.

When a small male encounters a large female, it may be beneficial for that male to spend
more time courting her or to pursue her more aggressively if such plastic changes enhance the probability of mating.

In some cases, a behavior may form during an animal’s development. Immelmann and Beer (1989) refer to the development of an individual’s behavior as it grows as ontogeny. Development of courtship behaviors may or may not entail learning, a process where changes in individual behavior are evidenced as a result of experience (Thorpe 1956).

Experience has been defined as the reactions an individual develops in response to stimuli it has encountered and learned about (Heymer 1977). An animal’s previous courtship experience may have a bearing on its future courtship behavior. This has been shown in zebra finches, *Taeniopygia guttata*, where females change their mate preference based on previous mating experience (Collins 1995). More successful reproductive strategies may also develop with experience. For example, female birds mating for the first time have less reproductive success than older, more experienced females (Domjan and Hollis 1988). This phenomenon has also been noted in elephant seals (Reiter et al. 1981). Smith et al. (1995, unpublished data) raised desert tortoises on a special diet which allowed them to reach adult size at five to six years, instead of the typical 12 to 20 years needed to attain maturity in wild tortoises. These researchers suggest that naive desert tortoises are not as competent at mating as more experienced tortoises. When the fast-growing tortoises were allowed to mate with wild adults, some unusual courtship behaviors appeared (Smith et al. 1995, unpublished data). Fast-growing females were aggressive towards males the first few times they were placed together, but this behavior soon stopped. Fast-growing males were not observed to court females until the third day.
they were placed together. It is possible that a change in courtship behavior occurs, as a result of courtship experience or perhaps a cessation of aggression. Conversely, it is possible that the fast growth of these tortoises was the cause of these altered courtship behaviors.

A juvenile spur-thighed tortoise, *Geochelone sulcata*, showed sexual behavior before it had developed secondary sexual characteristics. The behaviors it exhibited were not as refined as in adult males, thus this male was not successful in mating (Grubb 1971). Mahmoud (1967) noted in several kinosternid turtle species that courtship took place only between sexually mature animals. While these observations appear to be in conflict, it is possible that younger turtles exhibit “courtship” behaviors, but that they do not exhibit them in the proper context. Courtship behaviors resulting in successful matings may occur when the animal is older, as a result of learning or developmental change and maturation.

Turtle courtship

Courtship in turtles is often initiated by the male, who may be attracted by movements of the female. In all species of turtles, males must exhibit ‘following’ behavior in order for copulation to occur (Norris 1996). Courtship behaviors common in turtles include head bobbing and biting. A male turtle must subdue or immobilize the female enough that she will allow mounting and copulation. It is likely that males are not truly “subduing” or “immobilizing,” but rather inducing or eliciting cooperative behaviors in the female. However, as the terms subduing and immobilizing have been
used widely in the literature, they will be used here also.

A subduing method used widely by turtles is to bite at the female’s head, shell, and legs (Pough et al. 1998). In all species, the male cloaca must come into contact with the female’s cloaca for intromission to occur. It is thought that causing the female to pull in her head and forelimbs makes it harder for the female to keep her cloacal region closed off (Obst 1988), which in turn makes it easier for intromission to occur. Typically, the male mounts the female so that the male’s plastron rests against the female’s carapace.

There are several types of signals important in turtle courtship, including scent, tactile stimulation, visual signals, and in limited cases, sound. Scent plays a vital role in courtship of turtles. These chemical signals can be transmitted through air or water. Musk glands, chin glands, and cloacal odors are all sources of scents. Numerous testudinids can identify the species, sex, and even reproductive state of an individual by sniffing cloacal odors (Pough et al. 1998). For many tortoises, investigation of a female’s cloacal region is a prerequisite to male courtship (Auffenberg 1977). Chin gland secretions in *Gopherus*, the gopher tortoises, may provide cues about sex recognition (Winokur and Legler 1975). These secretions, specifically the fatty acids in them, may also allow *Gopherus* tortoises to distinguish familiar from unfamiliar males (Alberts et al. 1994). After sniffing the cloacal region of the female, a male tortoise may secondarily sniff her head (Alderton 1988).

Various tactile signals may be necessary for a successful mating. Some chelid turtles rub the barbels on their chins together (Murphy and Lamoreaux 1978). Other turtles, such as the male green turtle, *Chelonia mydas* (Ernst et al. 1994), may participate in head rubbing. Many turtles bite; most often the male bites the female but bites may be
reciprocated by the female in some aquatic species such as the alligator snapping turtle, *Macroclemys temminckii* (Grimpe 1987). When a male smells parts of a female’s body, his nose may touch or probe the female. Titillation occurs in some aquatic emydid turtles, where the long claws of the forelimbs are vibrated rapidly at the face of the mate. The rate of titillation is species-specific (Goin et al. 1978). Titillation may increase the female’s receptivity to mating (Pough et al. 1998). Some tortoise males ram females as an attempt to subdue them. Water gulping and expelling from the male’s nostrils occurs in some aquatic species such as Blanding’s turtle, *Emydoidea blandingii* (Baker and Gillingham 1983), and also in *Emydura subglobosa* (Norris 1996) and *E. macquarii* (Murphy and Lamoreaux 1978). Many male turtles grasp or scrape the shell of the female while mounted. Before intromission, the tails often interlock or are adjusted for proper cloacal contact. All of these tactile signals may have bearing on the success of a courtship bout.

A very common visual signal in many turtle species is head bobbing. This signal may be performed to attract attention, and in *Gopherus* it may help to disperse scent from chin glands (Auffenberg 1965). Communication by head bobbing may have evolved from olfactory movements (Auffenberg 1965). Head bobs may be vertical or horizontal; among some testudinids these movement patterns are species-specific (Eglis 1962, Auffenberg 1977). Some species such as the snapping turtle, *Chelydra serpentina*, engage in mutual head swaying (Legler 1955). Female *Emydura subglobosa* return the male’s head bobs (Norris 1996). Blinking eyes in male *Emydura subglobosa* (Norris 1996) and female *Trachemys scripta scripta* (Lovich et al. 1990) may also serve as a
visual stimulus to mating. In tortoises, the sight of a female raising up on her hind legs can provide another visual signal to the male that is important in mating.

In some aquatic species of the Emydidae, males face females and display species-specific color patterns on their necks and forelimbs (Pough et al. 1998). The color differences between sexes may also play some part in sex recognition while courting. Male spotted turtles (*Clemmys guttata*) have a tan chin and brown eyes while females have a yellow chin and orange eyes (Obst 1988). Breeding male *Geochelone travancorica* exhibit a bright red color around the eyes and nares (Auffenberg 1964a). Males of some tropical Asian river turtles show great color changes during the mating season (Halliday and Adler 1986). Any of these color differences may serve as visual stimuli important to mating.

Audio signals may play some role in the courtship of certain species of tortoises, although advertisement calls are not known (Pough et al. 1998). Male *Geochelone denticulata* from South America vocalize while pursuing and copulating with females. The Galapagos tortoise may produce loud bellows when copulating (Goin et al. 1978).

Male turtles may have special anatomical features which enhance their mating capabilities. Male turtles have longer tails with the cloacal opening situated more distal to the body; the female has a shorter tail with a more proximal cloacal opening. This difference in position facilitates intromission. In some aquatic species, males have long claws which are used for titillation in courtship and grasping the female's shell during mounting. Rough patches on a kinostemid male's inner rear legs are used for clasping the female's tail (Mahmoud 1967). Males often have concave plastrons which enhance a male's ability to stay mounted on a domed female's carapace. Female North American
eastern box turtles. *Terrapene carolina*, clamp their kinetic plastron shut so that the mounted male’s hind feet are held to keep him from falling off (Ernst et al. 1994).

Few authors have quantified courtship and mating behaviors in testudines. An example of videotaping turtle behaviors may be found in Jackson and Davis (1972b), where the recording of courtship behavior of Suwannee cooters, *Pseudemys (Chrysemys) concinna suwanniensis*, allowed measurement of the timing of specific behaviors. The authors state that courtship behavior was comprised of interaction for variable amounts of time, followed by a stereotypical display. Norris (1996) conducted a similar study on an aquatic, Australian side-necked turtle, *Emydura subglobosa*, in which sequences of courtship behaviors were quantified using videotape analysis. Certain sequences of behavior were found to be predictable. Recording interactions with videotape allows detailed quantitative study and can be used to estimate the amount of behavioral variation between and within individuals.

**Courtship in family Testudinidae**

Courtship behavior in testudinids includes head bobbing, biting, and ramming before mounting (Halliday and Adler 1986). Courtship and mating occur on land. In order to subdue a female, the male may bite the female’s head, shell, and legs; he may also use epiplastral ramming to subdue her. The female may signal that she is receptive by raising the posterior portion of her shell, or, she can lower this part of the shell to indicate lack of receptivity (Pough et al. 1998). Pough et al. (1998) state that members of family Testudinidae have a complex variety of signals used in courtship. Males initiate
courtship when attracted by a female’s movements or her scent (Pough et al. 1998). Males usually respond to other tortoises by either vertical or horizontal head movements, while females normally do not (Pough et al. 1998). The head movements in this family are species-specific (Eglis 1962), although the types (horizontal and vertical) are not necessarily correlated with phylogeny (Auffenberg 1965).

During courtship, the male gopher tortoise, *Gopherus polyphemus*, head bobs and circles the female. He bites her legs and shell, sometimes vigorously, until the female raises up on her hind legs. The male then mounts and intromission occurs (Auffenberg 1966). The *Testudo hermanni* male rams the shell of his apparently indifferent partner. As in *G. polyphemus*, the male does this until the female raises up on her hind legs. It is then that copulation may occur. In *T. hermanni*, courtship is reported to last up to several days (Street 1979).

Tortoises in genus *Gopherus* may rub chin gland secretions on enlarged scales of the front limbs. These chemical signals may also be dispersed by head movements (Pough et al. 1998). Chemical cues can also be important in species that do not possess these chin glands. Male *Geochelone carbonaria* and *G. denticulata* detect females first visually and then by chemical cues such as cloacal scent (Auffenberg 1965). If a male finds a sexually mature female, he can court her immediately or follow her for several days first (Pough et al. 1998).
Genus *Gopherus* courtship behavior

Male tortoises in genus *Gopherus* are unique among members of the Testudinidae in having actively secreting chin glands, while females of this species have undeveloped glands (Winokur and Legler 1975). These chin glands are seasonally active (Alberts et al. 1994). Chin gland secretions are composed of phospholipids, triglycerides, fatty acids, and cholesterol (Rose et al. 1969); the fatty acids are the critical components that play an important role in combat and courtship interactions in this genus (Rose et al. 1969, Rose 1970). Chin gland secretions are suspected of having pheromonal functions in the desert tortoise (Rose et al. 1969, Rose 1970). Rose (1970) contended that secretions elicit combat behavior in other males and serve as a "male-female" attraction in females. More recently, Alberts et al. (1994) suggested that tortoises differentiate between familiar and unfamiliar males by their chin gland secretions. The enlarged glands of males may additionally serve as a visual cue of a male's sexual readiness (Rose et al. 1969).

Weaver (1970) described courtship behavior in wild *Gopherus berlandieri*, with behaviors divided into four stages: trailing (lasting a few minutes to one hour); a period where the male overtakes the female, including biting the female on the head, front limbs, and anterior carapace and also ramming the female's shell (predominantly ramming her sides); a stage where the male attempts to mount the female; and lastly a stage of coition (which lasts no longer than 10 minutes). Weaver (1970) did not however perform detailed quantitative analyses on the amount of variation within and between males. Weaver also did not make any reference to male or female body size.
The description of courtship behavior in *Gopherus polyphemus* by Auffenberg (1966) is similar in its lack of quantifying behavioral variability. The qualitative description of courtship is similar to that in *G. berlandieri*, except that males of *G. polyphemus* bite the female's gular projections and female *G. polyphemus* may initiate courtship.

Black (1976) divided *Gopherus agassizii* courtship into stages. He listed (1) the approach, (2) trailing the female, (3) high-intensity head bobbing, circling, biting, and rams by the male to make the female withdraw, (4) mounting and possible copulation, and (5) the male falls off or the female moves away. Black stated that trailing can last a few minutes to several hours, and that mounting rarely exceeds 10 minutes.

Past studies of courtship and mating behaviors in *G. agassizii* have been anecdotal or incomplete (e.g. Householder 1950, Stuart 1954). A recent study provides an extensive list of *G. agassizii* behaviors (Ruby and Niblick 1994). However, these authors did not document variation in courtship behaviors. The intent of this research was to describe the sources and amount of variations in the behaviors described by Ruby and Niblick (1994).

Hypotheses

The following hypotheses about causes of variation in male courtship were tested for desert tortoises using data collected at the Desert Tortoise Conservation Center, Clark County, Nevada:

1. Male courtship behaviors change with mating experience.
2. Variation in courtship behaviors among individuals results from differences in male size and stage of ontogeny.

3. For a particular size, male tortoises exhibit behavioral plasticity and alter their courtship behaviors depending on the size of the female encountered.

4. Unsuccessful matings are the result of different behaviors than successful matings.
CHAPTER 2

METHODS

Studies were conducted at the Desert Tortoise Conservation Center (DTCC), a 640-acre research facility located near Las Vegas in Clark County, Nevada. The vegetation is dominated by creosote bush, *Larrea tridentata*, and bur sage, *Ambrosia dumosa*. All research animals were removed from construction sites in the Eastern Mojave Desert in 1990 and 1991 and have since been housed at the DTCC. Seven female and seven male tortoises in 1996, and 16 female and 15 male tortoises in 1997 were maintained in 7.4 m by 7.4 m outdoor semi-natural enclosures. Female tortoises were housed singly or in groups of two or three; males were housed individually. Tortoises received daily water from watering stations and had continuous access to Bermuda grass sod plots and alfalfa hay. A nutritional supplement was provided once or twice a week. Natural vegetation and artificial burrows were present in each enclosure.

A protocol for desert tortoise behavioral research (Number R701-0596-122) was approved by the Animal Care and Use Committee of the University of Nevada Las Vegas on July 23, 1996. Permission to make behavioral observations and to employ general husbandry practices was granted by the Desert Tortoise Conservation Center under their
U.S. Fish and Wildlife Service Endangered / Threatened Species Permit, issued in accordance with Section 10(a) of the Endangered Species Act.

All research tortoises had previously tested negative for URTD (upper respiratory tract disease), a mycoplasmal infection of concern in this threatened species. In addition, tortoises that showed signs of possible illness were not used in any interactions. In Fall 1996 and Summer 1997, maximum carapace length (MCL) was measured to the nearest millimeter and mass to the nearest gram for each tortoise. Each tortoise had a unique identification number marked on its carapace.

The term "size" is used with the assumption that the maximum carapace length (MCL) of a tortoise is positively correlated with its age. This assumption is complicated by uncontrolled factors, such as genetic make-up and quality of diet (and thus growth rate), which is variable. In addition, growth rates of desert tortoises vary geographically (Germano 1992). Three size categories of sexually mature animals, after Turner and Berry (1984), were used in this study and are listed in Table 1.

An individual tortoise was not involved in more than one interaction per day, in order to reduce chances of sexual satiation or excessive energy use by males or females. However, it has been noted that wild tortoises may have several sexual encounters in a single day (Lesley DeFalco, 1996, personal communication).

Experimental encounters began when a male and female tortoise, each randomly selected from all active tortoises, were placed inside a 3.2 m by 3.5 m interaction arena made of cement blocks. All interactions between tortoises were recorded on video tape with a Sony Video 8 video camera. Time, accurate to one second, was imprinted continuously on each video tape. When tortoises stopped interacting, recording stopped.
Table 1. Three size categories of sexually mature desert tortoises, *Gopherus agassizii* (from Turner and Berry 1984).

<table>
<thead>
<tr>
<th>Tortoise Size Class</th>
<th>Maximum Carapace Length (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Subadult</td>
<td>180 - 207</td>
</tr>
<tr>
<td>Adult 1</td>
<td>208 - 239</td>
</tr>
<tr>
<td>Adult 2</td>
<td>240 and greater</td>
</tr>
</tbody>
</table>
and tortoises were returned to their resident enclosures. Tortoises that did not court after approximately five minutes in the arena were returned to their enclosures. Video recording was conducted in early morning in the summer months to avoid heat stress to the tortoises.

Classifications of social behaviors in the ethogram presented by Ruby and Niblick (1994) were used as a tool to help quantify the variation in courtship behaviors observed in male desert tortoises. Specific behaviors described by Ruby and Niblick (1994) are denoted here by single quotation marks.

Courtship behaviors of several turtle species have been divided into phases or stages (i.e., Evans 1953, Auffenberg 1964b, Jackson and Davis 1972a). Male courtship in this study was divided into three phases, using elements from Auffenberg (1966), Weaver (1970), and Black (1976). I defined these distinct phases in the following manner. Phase 1. Trailing: the male ‘approaches’ and head bobs at the female. The female may then turn sideways in a ‘side-display’, and then may walk, indifferent to the male ‘trailing’ behind her. Phase 2. Subduing: the male head bobs more vigorously and actively overtakes the female and subdues her by ‘biting’, ‘ramming’, and scraping her shell with his claws. The female ‘rotates’ away from the male and withdraws into her shell. Phase 3, Mounting: the male ‘mounts’ the female’s shell, ‘hops’ to stay in place, and may copulate. The female can actively struggle or may remain passive during this third phase.

Social behaviors I noted during each courtship phase are listed in Table 2. Not all possible behaviors for each phase are listed here. In addition, some behaviors may be seen in two or more phases. In addition to the social behaviors listed in Table 2, tortoises
Table 2. Typical desert tortoise courtship behaviors observed in Phases 1, 2, and 3. This list is not an exhaustive one. Terms in single quotation marks are described by Ruby and Niblick (1994). Those terms in double quotation marks represent behaviors described in this paper.

<table>
<thead>
<tr>
<th>Phase</th>
<th>Male</th>
<th>Female</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phase 1 (Trailing)</td>
<td>&quot;approach*&quot;</td>
<td>&quot;side-display*&quot;</td>
</tr>
<tr>
<td></td>
<td>&quot;trailing*&quot;</td>
<td>&quot;head jerk in&quot;</td>
</tr>
<tr>
<td></td>
<td>&quot;level headbobs&quot;</td>
<td></td>
</tr>
<tr>
<td></td>
<td>&quot;elevated headbobs&quot;</td>
<td></td>
</tr>
<tr>
<td></td>
<td>&quot;exploratory sniff&quot;</td>
<td></td>
</tr>
<tr>
<td>Phase 2 (Subduing)</td>
<td>&quot;nip*&quot;</td>
<td>&quot;rotate*&quot;</td>
</tr>
<tr>
<td></td>
<td>&quot;hold bite*&quot;</td>
<td>&quot;head jerk in&quot;</td>
</tr>
<tr>
<td></td>
<td>&quot;front ram&quot;</td>
<td>&quot;turn head away&quot;</td>
</tr>
<tr>
<td></td>
<td>&quot;side ram&quot;</td>
<td>&quot;turn body away&quot;</td>
</tr>
<tr>
<td></td>
<td>&quot;bite-ram&quot;</td>
<td></td>
</tr>
<tr>
<td></td>
<td>&quot;level headbobs&quot;</td>
<td></td>
</tr>
<tr>
<td></td>
<td>&quot;elevated headbobs&quot;</td>
<td></td>
</tr>
<tr>
<td></td>
<td>&quot;gape&quot;</td>
<td></td>
</tr>
<tr>
<td></td>
<td>&quot;circling&quot;</td>
<td></td>
</tr>
<tr>
<td></td>
<td>&quot;scrape&quot;</td>
<td></td>
</tr>
<tr>
<td>Phase 3 (Mounting)</td>
<td>&quot;mount*&quot;</td>
<td>&quot;head in and out&quot;</td>
</tr>
<tr>
<td></td>
<td>&quot;hop&quot;</td>
<td>&quot;head swing&quot;</td>
</tr>
<tr>
<td></td>
<td>&quot;shell scratch&quot;</td>
<td></td>
</tr>
<tr>
<td></td>
<td>&quot;pull head in&quot;</td>
<td></td>
</tr>
<tr>
<td></td>
<td>&quot;ejaculate&quot;</td>
<td></td>
</tr>
<tr>
<td></td>
<td>&quot;copulation&quot;</td>
<td></td>
</tr>
</tbody>
</table>
commonly exhibit locomotor and maintenance behaviors such as 'sit,' 'stand,' 'climb,' and various forms of 'walk,' as described by Ruby and Niblick (1994). Females especially exhibit foraging behaviors such as 'food bite,' and 'substrate sniff.'

At the time of each interaction, I recorded air temperature at 10 cm above ground level, whether the male's chin glands were enlarged and/or visibly secreting, which sex initiated the interaction (that is, which sex walked directly toward the other one first), whether ejaculations were observed, whether the female's cloacal area was wet at the end of the interaction, and when possible to observe, whether intromission occurred.

Interactions recorded on video camera were reviewed using a Sony Video 8 EVO-540 Video Cassette Recorder in combination with a 19" Sony analytical PVM 19540 Color Video Monitor. I noted the following: amount of time spent in Phases 1 and 2 before the first mount; duration of the first mount (Phase 3); total duration of Phases 1, 2, and 3; percent of total time spent in each phase; number of rams and bites before the first mount; total number of rams and bites; location of each bite on the female's body; number of times the male mounted the female; and amount of time the male spent with the female in Phases 1 and 2 after the last mount. Occasionally, some behaviors were not visible on the videotape due to the camera's relative orientation to the interacting pair. When a male bit a female in a place that was not visible, this was recorded in the 'bite unknown' category.

Because I could not always clearly distinguish between the two, I recorded both types of bites described by Ruby and Niblick (1994) ('nip' and 'hold bite') simply as 'bite.' Similarly, I did not differentiate between 'front ram' and 'side ram' but counted
both as “ram.” Types of head bobs, as described by Ruby and Niblick (1994), were not distinguished for this study, due to time constraints.

Some social behaviors in Table 2 are momentary events (for example ‘ram’), while others are behavior states (such as ‘trailing’). This distinction is described by Martin and Bateson (1993) and Altmann (1974). Momentary events were counted individually and the durations of behavior states were recorded for each interaction.

For all “complete” encounters analyzed (n = 51), I calculated the probability of mating success by size class. (A “complete” interaction is defined here as one in which all 3 courtship phases occur, where Phase 1 is Trailing, Phase 2 is Subduing, and Phase 3 is Mounting.) I noted the number of interactions initiated by the male, the female, or both. Initiation involved one animal directly approaching another. I calculated mean values for duration of phases and number of bites and rams. I also determined the location on the female’s body for each bite.

For Hypothesis 1, the behaviors of males in different size classes were examined to see how size and experience influence behavior. Each of three males in size class Adult 1 and each of six Adult 2 males was paired with four randomly chosen females in size classes Adult 1 and Adult 2. Changes with experience were compared between male size classes for duration of Phases 1, 2, and 3; total duration; percentage of total courtship time spent in each phase; number of bites; and number of rams using a repeated measures ANOVA with temperature as a covariate.

For Hypotheses 2 and 3, male and female size classes were compared for duration of Phases 1, 2, 3, and total duration using an analysis of covariance, with temperature as the covariate. Percentage of total courtship time spent in each phase, number of rams,
number of bites, rams per minute in Phase 2, and bites per minute in Phase 2 were also compared with an analysis of covariance, with temperature as the covariate.

For Hypothesis 2, I used the first complete interaction for each male that had first been paired with a female of size class Adult 1 (n = 10). An analysis of covariance, with temperature as the covariate, was used to compare behaviors of males in size classes Adult 1 and Adult 2. Males paired with females of other size classes were not analyzed statistically due to small sample size (Subadult, n = 0; Adult 2, n = 7).

For Hypothesis 3, I also used only the first complete interaction for each male. Males in size class Adult 2 were the only group with a large enough sample size of behaviors to be compared statistically (n = 8). An analysis of covariance, with temperature as the covariate, was used to compare the behavior of males in size class Adult 2 when they were presented with females of two different size classes. Behaviors of males in other size classes (Subadult and Adult 1) were not analyzed statistically (n = 4 and n = 5, respectively).

For Hypothesis 4, I analyzed only the first complete interaction of each male to avoid the confounding factor of experience. I excluded interactions with questionable success. There were a total of 7 unsuccessful and 11 successful interactions in this data set. I defined “successful” as a mating in which copulation occurred (scored as 1) and “unsuccessful” as a mating in which copulation did not occur (scored as 0). I compared duration of Phases 1, 2, and 3, total duration, number of rams, and number of bites using an analysis of covariance, with temperature as the covariate. I also compared percentage of total courtship time spent in each phase for both successful and unsuccessful matings.
in a similar manner. Although female-female and male-male interactions were recorded.

I have not analyzed them in this study.
CHAPTER 3

RESULTS

In this study, I observed several behaviors not described by Ruby and Niblick (1994). These were "bite-ram," where a male simultaneously bit at a female and lunged forward with his body; "kick sand," where a male or female kicked dirt backwards with a front limb, similar to the description for *Gopherus polyphemus* by Hailman et al. (1991); and "scrape," where a male scraped his claws along a female's shell during Phase 2 (Subduing), usually while circling and trying to keep up with the rotating female. This is different from the 'shell scratch' noted by Ruby and Niblick (1994) during mounting, where the male scratches the female's carapace using right and left front legs alternately. Two other behaviors not described by Ruby and Niblick (1994) are "pull head in" and "ejaculate," both of which occur during Phase 3 (Mounting). The male pulls his head partly or completely into his shell as he ejaculates. Ejaculation may occur inside the female's cloaca or external to her cloaca, and is almost always accompanied by "pull head in." I did not see the 'side-display' as Ruby and Niblick (1994) described it, where a female turned sideways, then faced the male, then turned sideways again. The females in this study simply turned perpendicular to the male.
A form of vocalization was observed once in a wild female tortoise (243 mm MCL) and once in a captive female (270 mm MCL). The sound was somewhat like breathing in heavily and simultaneously opening and closing the mouth as if chewing. The wild tortoise that vocalized appeared to direct it towards me, as I observed it and another tortoise simultaneously digging a single burrow. The captive female tortoise approached and sniffed my boot and then vocalized.

Behaviors not described by Ruby and Niblick (1994), noted here by double quotation marks, occurred in the following frequencies in complete courtship interactions: "bite-ram," 32 of 51 interactions (62.7%), and "scrape." 51 of 51 interactions (100%). "Kick sand" was performed by males during Phase 2. 6 of 51 interactions (11.8%), by females during Phase 1. 4 of 51 interactions (7.8%), by females during Phase 2. 3 of 51 interactions (5.9%), and by females during Phase 3. 4 of 51 interactions (7.8%) (Table 3). In addition, there were several instances where females pushed back at a courting male. This "push back" behavior by females, not described by Ruby and Niblick (1994), occurred in 4 of 51 (7.8%) complete interactions and in one complete interaction in captivity which was not recorded on video tape. "Pull head in" occurred in 37 of 51 (72.5%) complete interactions. During Phase 2, a male would occasionally bite a rock on the ground, or even his own gular horns or front leg. These bites were not included in bite counts. All "bite-ram" events were included in counts of bites for this analysis. It should be noted that most rams were "front rams"; "side rams" were rare.

Ten of 61 matings analyzed were incomplete, that is, they consisted of only Phase
Table 3. Frequency of behaviors not described by Ruby and Niblick (1994) in desert tortoise courtship. Frequencies were calculated from all complete interactions (those with all 3 phases) (n = 51) of experimentally paired captive desert tortoises. See text for descriptions of each behavior.

<table>
<thead>
<tr>
<th>Behavior</th>
<th>Performer</th>
<th>Courtship Phase</th>
<th>Frequency of Occurrence</th>
</tr>
</thead>
<tbody>
<tr>
<td>&quot;Bite-Ram&quot;</td>
<td>Male</td>
<td>2</td>
<td>32/51 (62.7%)</td>
</tr>
<tr>
<td>&quot;Kick Sand&quot;</td>
<td>Male</td>
<td>2</td>
<td>6/51 (11.8%)</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>1</td>
<td>3/51 (5.9%)</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>2</td>
<td>3/51 (5.9%)</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>3</td>
<td>4/51 (7.8%)</td>
</tr>
<tr>
<td>&quot;Scrape&quot;</td>
<td>Male</td>
<td>2</td>
<td>51/51 (100%)</td>
</tr>
<tr>
<td>&quot;Push Back&quot;</td>
<td>Female</td>
<td>2</td>
<td>4/51 (7.8%)</td>
</tr>
<tr>
<td>&quot;Pull Head In&quot;</td>
<td>Male</td>
<td>3</td>
<td>37/51 (72.5%)</td>
</tr>
</tbody>
</table>
or Phases 1 and 2, without progressing to Phase 3. Five of these 10 incomplete interactions were by one male (230 mm MCL). The others were from 5 different individual males. Eight of the incomplete interactions occurred in May, and two in October. In these ten incomplete matings, "kick sand" was performed by females in Phase 1 in three interactions, and by a male in Phase 1 in one interaction.

The percent of successful matings was categorized by month as well as for all matings (Table 4). The number of interactions for each month are indicated in parentheses. Only complete interactions are included in this calculation.

Males initiated 30 of 51 (58.8%) complete encounters; females initiated 9 of 51 (17.6%); and both tortoises initiated 12 of 51 (23.5%) interactions (Figure 1).

The percent of mating success based on size class was calculated and is shown in Table 5 for all complete interactions. Of the female and male size class combinations with more than one complete mating, the highest mating success was seen in Female Adult 1 / Male Adult 2 combinations (100%; Table 5).

When complete interactions from all size classes were included, the mean time (± SE) spent in Phases 1, 2, and 3 was 12.75 ± 1.75 min, 11.11 ± 0.86 min, and 17.13 ± 1.17 min, respectively. Total interaction time averaged 41.00 ± 2.15 min (Figure 2). The percentage of total courtship time (± SE) spent in each phase averaged 29.7 ± 3.1% in Phase 1, 27.9 ± 2.0% in Phase 2, and 42.3 ± 2.3% in Phase 3 (Figure 3). Number of rams and bites (± SE) averaged 17.3 ± 3.4 and 85.2 ± 9.1, respectively (Figure 4), and the number of rams and bites per minute of Phase 2 (Subduing) (± SE) averaged 1.5 ± 0.2 and 8.0 ± 0.7, respectively (Figure 5). The average percentage of bites delivered to different areas of the female were as follows: to female's front leg, 37.0 ± 3.4%; to female's face,
Table 4. Percent of matings which appeared to be successful (sample size) in experimental pairings of captive desert tortoises, categorized by month. The overall percent of matings appearing successful is indicated in the column ‘Total.’ Only complete interactions (those with all 3 phases) are included (n = 51).

<table>
<thead>
<tr>
<th></th>
<th>Mar</th>
<th>Apr</th>
<th>May</th>
<th>Jun</th>
<th>Jul</th>
<th>Aug</th>
<th>Sep</th>
<th>Oct</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>67%</td>
<td>78%</td>
<td>38%</td>
<td>71%</td>
<td>100%</td>
<td>100%</td>
<td>100%</td>
<td>63%</td>
<td>69%</td>
</tr>
<tr>
<td></td>
<td>(3)</td>
<td>(9)</td>
<td>(13)</td>
<td>(7)</td>
<td>(4)</td>
<td>(2)</td>
<td>(5)</td>
<td>(8)</td>
<td>(51)</td>
</tr>
</tbody>
</table>
Figure 1. Percentage of interactions initiated by female, male, and both sexes in all complete interactions (those with all 3 phases) (n=51) of experimentally paired captive desert tortoises.
Table 5. Percent of successful matings (sample size) by size class in experimentally paired captive desert tortoises. Only complete interactions (those with all 3 phases) are included here (n = 51).

<table>
<thead>
<tr>
<th></th>
<th>Female Subadult</th>
<th>Female Adult 1</th>
<th>Female Adult 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male Subadult</td>
<td>0% (1)</td>
<td></td>
<td>0% (1)</td>
</tr>
<tr>
<td>Male Adult 1</td>
<td>100% (1)</td>
<td>46% (13)</td>
<td>80% (5)</td>
</tr>
<tr>
<td>Male Adult 2</td>
<td>100% (13)</td>
<td>65% (17)</td>
<td></td>
</tr>
</tbody>
</table>
Figure 2. Mean time (+/- SE) spent in each courtship phase and total time for all complete interactions (those with all 3 phases) (n=51) and all size classes of experimentally paired captive desert tortoises.

Figure 3. Mean percent of total time (+/- SE) spent in each courtship phase for all complete interactions (those with all 3 phases) (n=51) in all size classes of experimentally paired captive desert tortoises.
Figure 4. Mean number (+/- SE) of rams and bites observed in Phase 2 (Subduing) for all complete interactions (those with all 3 phases) (n=51) and all size classes of experimentally paired captive desert tortoises.

Figure 5. Mean number (+/- SE) of rams and bites per minute in Phase 2 (Subduing) for all complete interactions (those with all 3 phases) (n=51) and all size classes of experimentally paired captive desert tortoises.
5.6 ± 1.0%; to female's shell, 45.7 ± 3.8%; to female's rear legs, 0.7 ± 0.3%; to female's gular horns, 0.4 ± 0.3%; and to a part of the female not visible in the video recording, 10.6 ± 1.1% (Figure 6). Following mounting, a male would often exhibit Phase 1 and sometimes Phase 2 behaviors for up to several minutes. Phase 1 behavior after the last mount averaged 2.54 minutes (range = 0.00 - 35.38 min), while Phase 2 after the last mount averaged only 0.34 minutes (range = 0.00 - 5.98 min). These actions after the last mount were not included in analyses of phase durations.

For all complete interactions, temperature covaried negatively with phase durations and covaried positively with behavior counts and rates.

Behavioral variables used to test all hypotheses were either normally distributed or were transformed (log 10 or square root) to a normal distribution. Samples passed homogeneity of variance tests.

**Hypothesis 1**: Male courtship behaviors change with mating experience.

Using temperature (log 10 transformed) as a covariate, I found a significant effect of courtship experience on duration of Phase 1 (p = 0.035): Adult 1 males showed a decrease in duration of Phase 1, while Adult 2 males showed an increase in duration of Phase 1 (Figure 7). Adult 1 and Adult 2 males responded differently to Phase 1 with experience (p = 0.0034). No effect of experience was seen for Phase 2 (Figure 8). Phase 3 also showed no significant changes with experience (Figure 9). Total time spent in courtship did not change with experience for either size class of male (Figure 10). The percentage of total time spent in Phase 1 changed with experience (p = 0.0038) and was
Figure 6. Mean percent (+/- SE) of total bites to locations on females for complete interactions (those with all 3 phases) (n=50) in experimentally paired captive desert tortoises. Unknown category refers to bites in which location was not visible on the video recording. One complete interaction is not included here since there were no bites.
Figure 7. Mean time (+/- SE) spent in Phase 1 by Adult 1 and Adult 2 males in four consecutive complete matings of captive desert tortoises.

Figure 8. Mean time (+/- SE) spent in Phase 2 by Adult 1 and Adult 2 males in four consecutive complete matings of captive desert tortoises.

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Figure 9. Mean time (± SE) spent in Phase 3 by Adult 1 and Adult 2 males in four consecutive complete matings of captive desert tortoises.

Figure 10. Mean total time (± SE) spent in courtship by Adult 1 and Adult 2 males in four consecutive complete matings of captive desert tortoises.

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different for Adult 1 and Adult 2 males (p = 0.002). With increased experience, Adult 1 males showed a decrease in percent of total time spent in Phase 1, while Adult 2 males showed a slight increase (Figure 11). No significant effect of experience was apparent for percent of total time in Phase 2 (Figure 12). The percent of total time spent in Phase 3 changed significantly with courtship experience (p = 0.00002) and affected Adult 1 and Adult 2 males differently (p = 0.0013). Adult 1 males showed a sharp increase in percent of total time spent in Phase 3 between the 2nd and 3rd interactions, while Adult 2 males remained at a fairly constant percent (Figure 13).

The effect of experience on number of rams (log 10 transformed) was not significant, but Adult 1 and Adult 2 males responded differently (p = 0.013). Adult 1 males showed a sharp decrease for number of rams between Interactions 2 and 3, while Adult 2 males first increased, then decreased the number of rams (Figure 14). The number of rams per minute (log 10 transformed) in Phase 2 did not change with experience (Figure 15). The number of bites (log 10 transformed) was not significantly changed with experience but Adult 1 and Adult 2 males responded differently (p = 0.026). Adult 1 males showed a variable pattern in number of bites, while Adult 2 males increased and then decreased the number of bites (Figure 16). The number of bites per minute in Phase 2 similarly did not change with experience (Figure 17). Since experience resulted in some differences in behavior, only the first complete interaction by each male will be used for the remaining hypotheses.

**Hypothesis 2:** Variation in courtship behaviors between individuals results from differences in male size.
Figure 11. Mean percent of total time (± SE) spent in Phase 1 by Adult 1 and Adult 2 males in four consecutive complete matings of captive desert tortoises.

Figure 12. Mean percent of total time (± SE) spent in Phase 2 by Adult 1 and Adult 2 males in four consecutive complete matings of captive desert tortoises.
Figure 13. Mean percent of total time (+/- SE) spent in Phase 3 by Adult 1 and Adult 2 males in four consecutive complete matings of captive desert tortoises. *
Figure 14. Mean number (+/- SE) of rams by Adult 1 and Adult 2 males in four consecutive complete matings of captive desert tortoises.

Figure 15. Mean number (+/- SE) of rams per minute in Phase 2 by Adult 1 and Adult 2 males in four consecutive complete matings of captive desert tortoises.
Figure 16. Mean number (± SE) of bites by Adult 1 and Adult 2 males in four consecutive complete matings of captive desert tortoises.

Figure 17. Mean number (± SE) of bites per minute in Phase 2 by Adult 1 and Adult 2 males in four consecutive complete matings of captive desert tortoises.
Behavior counts and courtship phase durations for males paired with Adult 2 females were not analyzed statistically due to small sample size, however, the means for behavior counts and durations were calculated and are shown in Table 6.

Temperature was used as a covariate in all analyses for this hypothesis. When paired with Adult 1 females, no significant differences were found between Adult 1 males and Adult 2 males for duration of Phases 1, 2, and 3, or total duration (Figure 18); in percentage of total time spent in each courtship phase (Figure 19); or in the mean number of rams or bites ($p = 0.818$ and $p = 0.056$, respectively) (Figure 20). There was no difference in mean number of rams per minute in Phase 2 by Adult 1 and Adult 2 males, but a significant difference was found between male size classes for number of bites per minute in Phase 2 ($p = 0.018$): Adult 2 males bit females significantly more frequently than did Adult 1 males (Figure 21).

**Hypothesis 3:** Male tortoises alter their courtship behaviors depending on the size of the female encountered.

Behavior count and courtship phase duration means for male Subadult and Adult 1 size classes are shown in Table 7, and were not statistically analyzed due to small sample size.

Temperature was used as a covariate for all analyses in this hypothesis. No significant differences were found in duration of phases or total duration for males interacting with females of size class Adult 1 and Adult 2 for (Figure 22), nor in percentage of total time spent in each courtship phase (Figure 23), number of rams and
Table 6. Means (± se) of behavior counts and courtship phase durations for two male size classes paired with females of size class Adult 2. Subjects were experimentally paired captive desert tortoises.

<table>
<thead>
<tr>
<th>Male Size Class</th>
<th>Female Adult 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sample Size (n)</td>
<td>3</td>
</tr>
<tr>
<td>Phase 1 (min)</td>
<td>15.2 (± 10.2)</td>
</tr>
<tr>
<td>Phase 2 (min)</td>
<td>13.7 (± 2.1)</td>
</tr>
<tr>
<td>Phase 3 (min)</td>
<td>20.8 (± 4.6)</td>
</tr>
<tr>
<td>Total Time (min)</td>
<td>49.6 (± 13.4)</td>
</tr>
<tr>
<td>Rams</td>
<td>46.0 (± 15.0)</td>
</tr>
<tr>
<td>Rams / Min Phase 2</td>
<td>3.4 (± 0.9)</td>
</tr>
<tr>
<td>Bites</td>
<td>103.3 (± 23.4)</td>
</tr>
<tr>
<td>Bites / Min Phase 2</td>
<td>7.6 (± 1.2)</td>
</tr>
</tbody>
</table>
**Figure 18.** Mean time (+/- SE) spent in each courtship phase and total time for Adult 1 🅱️ and Adult 2 🅱️ males paired with Adult 1 females. Subjects were experimentally paired captive desert tortoises.

**Figure 19.** Mean percent of total time (+/- SE) spent in each courtship phase and total time for Adult 1 🅱️ and Adult 2 🅱️ males paired with Adult 1 females. Subjects were experimentally paired captive desert tortoises.
Figure 20. Mean number (+/− SE) of rams and bites observed in Phase 2 (Subduing) for Adult 1 and Adult 2 males paired with Adult 1 females. Subjects were experimentally paired captive desert tortoises.

Figure 21. Mean number (+/− SE) of rams and bites per minute in Phase 2 (Subduing) for Adult 1 and Adult 2 males paired with Adult 1 females. Subjects were experimentally paired captive desert tortoises. *p=0.018
Table 7. Means (± SE) of behavior counts and courtship phase durations for two male size classes paired with two female size classes. Subjects were experimentally paired captive desert tortoises.

<table>
<thead>
<tr>
<th>Female Size Class</th>
<th>Male Subadult</th>
<th>Male Adult 1</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sample Size (n)</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Phase 1 (min)</td>
<td>5.0 (± 0.3)</td>
<td>4.1 (± 0.1)</td>
</tr>
<tr>
<td>Phase 2 (min)</td>
<td>15.7 (± 5.7)</td>
<td>14.4 (± 1.2)</td>
</tr>
<tr>
<td>Phase 3 (min)</td>
<td>15.3 (± 6.7)</td>
<td>15.1 (± 12.9)</td>
</tr>
<tr>
<td>Total Time (min)</td>
<td>36.0 (± 1.2)</td>
<td>33.5 (± 14.1)</td>
</tr>
<tr>
<td>Rams</td>
<td>38.0 (± 38.0)</td>
<td>73.5 (± 2.5)</td>
</tr>
<tr>
<td>Rams / Min Phase 2</td>
<td>1.8 (± 1.8)</td>
<td>5.1 (± 0.2)</td>
</tr>
<tr>
<td>Bites</td>
<td>58.5 (± 2.5)</td>
<td>86.5 (± 4.5)</td>
</tr>
<tr>
<td>Bites / Min Phase 2</td>
<td>4.2 (± 1.4)</td>
<td>6.1 (± 0.8)</td>
</tr>
</tbody>
</table>
Figure 22. Mean time (+/- SE) spent in each courtship phase and total time for Adult 2 males paired with Adult 1 and Adult 2 females. Subjects were experimentally paired captive desert tortoises.

Figure 23. Mean percent of total time (+/- SE) spent in each courtship phase for Adult 2 males paired with Adult 1 and Adult 2 females. Subjects were experimentally paired captive desert tortoises.
number of bites (Figure 24), or number of rams per minute in Phase 2 (Figure 25). Males in size class Adult 2 showed significantly higher rates of biting in Phase 2 towards females in size class Adult 1 than Adult 2 ($p = 0.011$). Males bit Adult 1 females at approximately twice the frequency of Adult 2 females (9.6 bites/min and 4.5 bites/min. respectively) (Figure 25).

**Hypothesis 4:** Unsuccessful matings are the result of different courtship behaviors than successful matings.

The average size of a male in an unsuccessful mating was significantly smaller ($p = 0.041$) than the average size of a male in a successful mating. The average size of a female was not different between unsuccessful and successful matings (Figure 26).

Using temperature as a covariate for all behavioral measurements. similar amounts of time were spent in Phase 1 in both unsuccessful and successful matings. Similarly, there was no difference in time spent in Phase 2 between successful and unsuccessful matings. Males in unsuccessful matings spent significantly less time in Phase 3 than males in successful matings ($p=0.001$). Total interaction time did not differ between successful and unsuccessful matings ($p = 0.060$) (Figure 27).

Percent of total time spent in Phases 1 and 2 was not different for successful and unsuccessful matings. Tortoises in successful matings spent a greater percentage of time in Phase 3 than tortoises in unsuccessful matings ($p = 0.0026$) (Figure 28).

Within Phase 2 (Subduing), the number of rams and bites by males in successful and unsuccessful matings was not statistically different ($p = 0.095$ and $p = 0.067$, respectively).
Figure 24. Mean number (± SE) of rams and bites observed in Phase 2 (Subduing) for Adult 2 males paired with Adult 1 and Adult 2 females. Subjects were experimentally paired captive desert tortoises.

Figure 25. Mean number (± SE) of rams and bites per minute in Phase 2 (Subduing) for Adult 2 males paired with Adult 1 and Adult 2 females. Subjects were experimentally paired captive desert tortoises. *p=0.011

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Figure 26. Mean maximum carapace length (MCL) (+/- SE) for unsuccessful and successful matings. Subjects were experimentally paired captive desert tortoises. *p=0.041
Figure 27. Mean time (+/- SE) spent in each courtship phase and total time for unsuccessful and successful matings. Subjects were experimentally paired captive desert tortoises. *p=0.001

Figure 28. Mean percent of total time (+/- SE) spent in each courtship phase for unsuccessful and successful matings. Subjects were experimentally paired captive desert tortoises. *p=0.0026

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respectively), however, males in unsuccessful matings rammed females approximately
twice more often than males in successful matings (Figure 29). The number of rams per
minute in Phase 2 was different between these two groups of animals (p = 0.044), with a
mean of 1.2 ± 0.4 in successful matings and 2.5 ± 0.6 in unsuccessful matings. The
number of bites per minute in Phase 2 in successful matings was greater than in
unsuccessful matings (p = 0.036): males in Adult 1 and Adult 2 size classes averaged
4.21 ± 0.81 and 9.59 ± 1.05 bites per minute, respectively (Figure 30).

Summary of Results

There was a seasonal pattern of mating success, with highest success from March
to April and July to September. Courtship experience affects Adult 1 males differently
than Adult 2 males: The behaviors of Adult 1 males seemed more variable at first, but
became more consistent with increased experience. The behaviors of Adult 2 males
remained fairly constant with increased experience. Adult 2 males bit females at a rate
significantly higher than the rate of Adult 1 males. Males bit Adult 1 females at a
significantly higher rate than they bit Adult 2 females. Males in successful complete
matings were significantly larger, spent more time in Phase 3, spent a greater percentage
of total courtship time in Phase 3, rammed females at a lower rate, and bit females at a
higher rate than males in unsuccessful complete matings.
Figure 29. Mean number (+/− SE) of rams and bites observed in Phase 2 (Subduing) in unsuccessful ⬤ and successful ⬤ matings. Subjects were experimentally paired captive desert tortoises.

Figure 30. Mean number (+/− SE) of rams and bites per minute in Phase 2 (Subduing) in unsuccessful ⬤ and successful ⬤ matings. Subjects were experimentally paired captive desert tortoises. *p=0.044, #p=0.036

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CHAPTER 4

DISCUSSION

Courtship behavior in *Gopherus agassizii* appears to follow the general pattern found in other tortoises, where head bobbing, biting, and ramming occur before mounting the female (Halliday and Adler 1986). Tortoises in general perform most of their courtship behaviors before mounting, unlike some turtle species which exhibit most of their courtship behaviors while mounted (Baker and Gillingham 1983).

I found that the average time spent in the mounting phase of courtship (17.13 min) was greater than that described for wild tortoises by other authors (rarely more than 10 minutes in *G. agassizii* (Black 1976) and never more than 10 minutes in *G. berlandieri* (Weaver 1970). The fact that the research tortoises used in my study had been in captivity and in an environment relatively free of predators for five to six years may have had some bearing on this. Since temperature negatively covaried with phase durations of courtship behaviors in *G. agassizii*, and the above authors did not report temperatures, the time spent in Phase 3 (Mounting) will not be directly compared here.

The seasonal reproductive cycle in *G. agassizii* described by Rostal et al. (1994) corresponds with my data in Table 4, where the greatest percentages of successful
matings are from March to April and July to September, with lower percentages of success in May and June. The ten incomplete interactions I analyzed took place in May and October. Interestingly, during the time that many females were gravid (mainly the month of May), males seemed able to 'sense' something different about these females, and did not court them as vigorously as they did at other times of the year, or they did not court at all.

The courtship behaviors of Adult 1 males were initially more variable, but became more consistent with increased experience. The behaviors of Adult 2 males remained fairly constant with increased experience. This could be explained by the likelihood that Adult 2 males are older and have had more matings (and thus more experience) prior to these trials, giving them time to become more consistent in courtship behaviors.

Adult 2 males bit females at a faster rate than Adult 1 males. One explanation might be that Adult 2 males are bigger than Adult 1 males, so it was easier for them to circle the rotating female and remain close to her. In contrast, Adult 2 males could have had more experience prior to these interactions and may have modified their behavior.

Males bit Adult 1 females at a faster rate than they bit Adult 2 females. This could be related to the smaller relative size of the Adult 1 females, which could make it easier for males to keep close as the females rotate. Conversely, the Adult 1 females might need more persuasion (in the form of more rapid bites) before allowing the males to mount.

Differences in courtship behaviors were noted between successful and unsuccessful matings. The duration of Phase 3 (Mounting) was significantly greater in successful matings. This may simply be due to the increased time needed for
intromission to occur, or it may reflect the female’s willingness to let the male remain mounted for a longer period of time due to his successful completion of courting. Successful matings involved more bites per minute in Phase 2, indicating that more vigorous displays are more successful. Support for this statement comes from Vinnedge and Verrell (1998), who found that in courtship displays of the salamander Desmognathus ocoee, the most persuasive males achieved the highest mating success. Information about behavioral differences associated with successful and unsuccessful matings in desert tortoises provides researchers with a more thorough understanding of the reproductive biology of this threatened species.

The data from my study supplement that of Ruby and Niblick (1994). In order for the desert tortoise to be more fully understood, studies on behavior should include wild populations. In my limited observations of wild matings (n = 3), courtship did not appear different in basic structure from my observations of captives. I noted in one wild interaction that the male rammed the female’s side, not the front of her shell as was more common in the captive interactions I have seen.

The female’s role in courtship has been largely unstudied in turtles. Lovich et al. (1990) studied the role of females in courtship in the yellow bellied slider, Trachemys scripta scripta. Females of this subspecies blink their eyes at males, rapidly stroke their front feet on or near the male’s head (titillation), investigate male cloacal areas, trail males, and orient towards males. The number of instances where reproductive behaviors were directed toward females was not different from the number of instances where reproductive behaviors were directed toward males. This suggests that females in this subspecies have an active role in mating (Lovich et al. 1990). Female loggerhead musk
turtles, *Sternotherus minor*, are also active during courtship: they may bite and flee from the male (Bels and Crama 1994). How important female behaviors are to courtship in *G. agassizii* is not yet known. My data suggests that females appear to have at least some input as to whether or not the mating will be successful. Unreceptive females may actively run away from courting males or may prevent intromission by holding the rear of their shell down. Females can actively struggle while a male mounts them, which can cause him to fall off or land on his back. Females in four of 51 interactions pushed back at the male while he was attempting to subdue her. Also, females initiated 17.6% of complete courtship interactions.

Members of genus *Gopherus* may begin courtship in the open, or sometimes at the entrance to a female’s burrow. In *G. polyphemus* and *G. flavomarginatus*, it has been reported that males head bob and court females at the burrow entrance and wait for the female to emerge (Bickett 1980, Lindquist and Appleton 1982, Appleton 1983, Douglass 1986). This has been reported in *G. berlandieri* and *G. agassizii* (Berry 1974, in Douglass 1986; Weaver 1970, in Douglass 1986), although I have not seen this behavior in *G. agassizii* in captivity or in the wild. I have, however, seen females enter burrows during courtship, effectively preventing a successful mating.

*Gopherus polyphemus* males are reported to bite the female’s gular horns frequently during courtship, whereas it was not seen by Weaver (1970) in *G. berlandieri*. Biting the female’s gular horns was uncommon in *G. agassizii*, occurring once in each of six courtship interactions (by 6 different males). This represents 0.14% of the sum of bites for all 51 complete interactions. Presently, all four *Gopherus* species are allopatric, although their predecessors were partly sympatric in the Pleistocene (Bramble 1971). It
is possible that this difference in location of bites played a role in a behavioral form of reproductive isolation during the Pleistocene sympatry between *Gopherus* species complexes.

The results of this study lend insight to the amount and sources of variability in tortoise reproductive behavior and heighten our understanding of the courtship behaviors of the desert tortoise. All of the hypothesized sources of variation (experience, behavioral plasticity, and size or ontogeny) were associated with differences in courtship behavior. Recent conservation efforts have included translocating desert tortoises from construction sites to more remote areas of the Mojave Desert in the hopes of creating self-sustaining populations. It is important to know that younger (smaller) males differ in their courtship success from older (larger) males. If both short-term and long-term reproductive success are required for the persistence of a population, it will be necessary to translocate both larger (older) and smaller (younger) males to prevent a decline in birth rate within local populations.

Quantifying the behaviors of a population of animals allows comparison with other populations and species, and in some cases can be used to infer species relationships (Wimberger and de Queiroz 1996). Future studies may compare behaviors between desert tortoise populations (such as Mojave and Sonoran populations) and the other species of *Gopherus*: *G. berlandieri*, *G. flavomarginatus*, and *G. polyphemus*. Population differences might be compared to geographic patterns of genetic variation (Lamb et al. 1989) and provide additional support for management procedures, such as the preservation of evolutionarily significant units. In addition, quantitative inter-specific and inter-generic comparisons could be studied for turtle courtship behaviors. This may
prove especially helpful in the description of poorly understood species. It is fundamental to study behavioral aspects of threatened and endangered species such as the desert tortoise, in order to more fully understand their life histories. and perhaps to enhance their chances of persistence through proper management and conservation programs.
REFERENCES


VITA

Graduate College
University of Nevada. Las Vegas

Rebecca Lynn Holte

Local Address:
Las Vegas, Nevada 89154

Degree:
Bachelor of Arts, Biology, 1995
Gustavus Adolphus College, Saint Peter, Minnesota

Special Honors and Awards:
Phi Beta Kappa, member since 1995
Best Student Poster Award, Desert Tortoise Council Annual Symposium. Tucson.
Arizona, April 1998.

Thesis Title: Analysis of courtship behaviors of the desert tortoise. Gopherus agassizii.

Thesis Examination Committee:
Chairperson, Dr. Charles Douglas, Ph. D.
Committee Member, Dr. Daniel Thompson, Ph. D.
Committee Member, Dr. Robert Winokur, Ph. D.
Graduate Faculty Representative, Dr. F. W. Bachhuber, Ph. D.