Herpetological Conservation and Biology 12(2):373–383.
Submitted: 10 December 2016; Accepted: 21 January 2017; Published: 31 August 2017.

Behavior and Conspecific Interactions of Nesting Gopher Tortoises (*Gopherus polyphemus*)

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***Abstract*.—Nesting behavior, including nest site selection, has important consequences for many egg-laying reptiles because it can influence egg depredation rates, embryonic development, and offspring characteristics. We investigated nesting behavior in a population of Gopher Tortoises (*Gopherus polyphemus*) inhabiting an old-growth Longleaf Pine (*Pinus palustris*) forest in southwest Georgia (USA) using time-lapse video cameras set to record nesting activity in front of tortoise burrows, where females often nest. Information on nesting in this species is primarily limited to frequency, seasonal timing, and location; actual nesting behavior remains incompletely described for wild individuals. Females engaged in nesting activity at their own burrows and at other burrows from 1000 to about 1800 during late May to mid June. Tortoises exhibited wide variation in nest site preparation activity, ranging from no preparation to circling and constructing a shallow depression. Nesting females faced away from burrows, braced with forelimbs, and used hindlimbs to dig nest cavities, arrange oviposited eggs, and initially cover nests. On average females spent 74 min constructing nests, but about twice as long manicuring nest sites thereafter. Manicuring females repeatedly nuzzled the ground, kicked dirt out of burrows onto nests and surrounding areas, and roughed up the soil, perhaps to assess and obscure olfactory and visual cues available to potential nest predators. Notably, on multiple occasions females abandoned nesting attempts in response to conspecifics. Additional observations of conspecific interactions at burrows, particularly aggressive mating attempts and female-female combat involving gravid individuals, further indicate that tortoises routinely interact in ways that can interfere with nesting and influence where individuals nest.**

Key Words.—Georgia; Longleaf Pine; nests; reproduction; reptile; social; turtle

Introduction

Nesting behavior can influence reproductive success and offspring quality in oviparous species. For example, nest-site selection by female turtles can determine incubation environment and affect embryonic development, hatching success, and offspring performance (Wilson 1998; Booth et al. 2013). In many turtles, nest temperature also determines offspring sex, which may be important when demographic or environmental characteristics benefit one sex over the other (Charnov and Bull 1977; Bull and Vogt 1979). In addition to carefully selecting nest sites, some turtles camouflage nests from predators or actively guard nests (Hailman and Elowson 1992; Agha et al. 2013 and references therein). External factors such as nest-site availability or human disturbance may influence nesting behavior (Roosenburg 1991; Johnson et al. 1996), but conspecific interactions are not thought to interfere with nesting activities in most turtles (but see Hughes and Richard 1974; Doody et al. 2009).

Gopher Tortoises (*Gopherus polyphemus*) inhabit dry upland areas along the Coastal Plain of the southeastern United States. Individuals center daily activities on long (often > 4 m) burrows that they excavate and use for thermoregulation, predator avoidance, rest, and other activities (Douglas and Layne 1978). In part because tortoises spend most of their time at burrows, these sites also serve as primary locations for mating and competitive intrasexual interactions (Douglas 1986; McRae et al. 1981; Diemer 1992; Johnson et al. 2007; Guyer et al. 2014). Additionally, in many populations, females often, perhaps predominantly, nest just in front of burrows in the mound of bare soil referred to as the burrow apron (Landers et al. 1980; Butler and Hull 1996; Epperson and Heise 2003; Hammond 2009; Lamb et al. 2013). Gopher Tortoises potentially prefer relatively sunlit burrow aprons or other warm bare ground areas as nest sites, but such sites may be less common in areas where fire suppression has allowed dense hardwood shrubs and small trees to dominate (Diemer 1986; Diemer and Moore 1993; Averill-Murray et al. 2014).

We investigated the nesting behavior of Gopher Tortoises in an old-growth forest dominated by an overstory of Longleaf Pine (*Pinus palustris*) and a diverse groundcover community composed of hundreds

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of native forbs and grasses. Although Gopher Tortoises have been studied extensively, aspects of their nesting behavior beyond frequency, seasonal timing, and location (e.g., cavity construction, egg laying) remain largely undescribed. Gopher Tortoise behaviors can be difficult to document due to the tendency of individuals from many populations to quickly hide in burrows when approached (Anderson 2001, Thomas Radzio, pers. obs.). Butler and Hull (1996) briefly observed two wild female Gopher Tortoises digging nest cavities, but both tortoises abandoned nesting attempts before ovipositing, apparently in response to researcher presence. The most complete account of an actual nesting event is for a single captive individual kept far north of the range of the species in Connecticut, USA (Kenefick 1954).

We used time-lapse video cameras to document the natural, undisturbed behaviors of nesting Gopher Tortoises before, during, and after oviposition. Our observations comprised nesting activity as well as interactions between tortoises, including gravid females, at nest sites. This work provides new insights into tortoise social interactions and how they might influence nesting activity in this secretive species.

Materials and Methods

Study site description.—We studied Gopher Tortoise nesting and conspecific interactions on Wade Tract (30°45'N, 84°0'W), an 80-ha old-growth ecological preserve located near Thomasville in southwestern Georgia, USA. Longleaf Pines, many greater than 200 y old, dominated the upper canopy (Platt et al. 1988). Ground cover included relatively few bare spots and was dominated by Wiregrass (*Aristida stricta*), oak (*Quercus* spp.), and other native plants (Christine Ambrose, unpbl. report). Wade Tract is located within Arcadia Plantation, a 957-ha area that consists primarily of mature (> 80 y) Longleaf Pine forest. Wade Tract is managed by Tall Timbers Research Station using frequent prescribed fire (≤ 2-y return intervals), and surrounding areas of Arcadia Plantation are burned at similar intervals. Previous work at Wade Tract reports a site-wide density of adult tortoises of 0.8 individuals/ha (Guyer et al. 2012). However, adult tortoise densities at locations within the site where we conducted observations were higher (Thomas Radzio, unpubl. data).

Observations of nesting and conspecific interactions.—We set time-lapse video cameras (Plotwatcher Pro, Day 6 Outdoors, Inc., Columbus, Georgia, USA) to record activity at tortoise burrows known or thought to potentially contain adult female tortoises. We attached cameras to wooden stakes and positioned them to monitor burrow entrances, burrow aprons, and surrounding areas. We programmed video cameras to record a time-stamped frame every 5 s during daylight hours, except for a very small number of days when we set video cameras to record a frame every 1 s. Tortoises did not appear to respond to the presence of cameras.

During mid-May to late-June 2013, video cameras monitored the activities of 10 female tortoises at their burrows, hereafter referred to as resident tortoises 1–10 that each could be individually identified by the presence of radio transmitters (used in another study) or unique shell markings. Resident females were monitored for 2–33 complete d (median = 20 d; complete day = video collected from at least 0600–1900, but usually dawn to dusk; all times reported in Eastern Standard Time). Additionally, cameras monitored activity at two other burrows, both occupied by adult males, for 5–11 complete d. We refer to tortoises that appeared at the burrows of resident tortoises as visitors.

From mid-May to mid-June, we visited tortoise burrows on most days to search for nests. In general, we spent little time at individual burrows, allowing tortoises to engage in natural, undisturbed activity and behavior throughout most of the day. We rarely dug into burrow aprons to locate nests, but instead relied on signs of potential nesting activity such as disturbance to burrow aprons and presence of fresh soil behind burrow entrances (Matt Hinderliter, pers. comm.). When we located a nest, we initially covered it with a small piece of hardware cloth, buried several cm below the soil surface, to protect eggs against predators (Radzio et al. 2017). Only in one of six instances where females completed a nest on video did we dig in burrow aprons or install a nest protector during the remaining daylight period following nesting. In that instance, we partially excavated the nest and covered it at 1900, more than 3 h after the female completed nesting. Therefore, we only minimally influenced nest manicuring activity. In most cases, we allowed cameras to continue recording tortoise activity at nest sites for several days following nest discovery.

Data analysis.—We viewed video recordings in GameFinder software (Day 6 Outdoors, Columbus, Georgia) and scored all nesting attempts, conspecific visits, and social interactions. We assessed whether females dug nest cavities and oviposited with their heads oriented non-randomly relative to burrow entrances (either facing at least partially toward or at least partially away from the burrow) using a binomial test. We also evaluated variation in the time that females spent in different stages of nesting (identified and described in Results) using a Kruskal-Wallis test. We used this nonparametric test because sample sizes were too small to assess assumptions of parametric procedures. We performed posthoc pairwise comparisons using

Table 1. Nesting observations, minimum number of nesting attempts away from own burrow (NA), minimum number of female-female interactions at potential nesting sites (burrows) 10 d preceding nesting (FFI), and minimum number of conspecific disruptions to nesting activity (includes disruptions during nest manicuring activity; CD) for individual Gopher Tortoises (*Gopherus polyphemus*) from a site in southwestern Georgia, USA, based on video recordings at burrow aprons. Asterisks indicate possible nesting activity away from own burrow.

Female	Nesting Observations	NA	FFI	CD
Resident 1	5 June 2013, 1146–1207: Attempted to nest at own burrow. Abandoned attempt, perhaps due to approaching rainstorm. 8 June 2013, 1009–1117: Nested successfully at own burrow. Two visiting males disrupted nest covering and manicuring.			2
Resident 2	7 June 2013, 1550–1622: Abandoned nesting attempt at own burrow. Large root observed in abandoned cavity. 7-14 June 2013: No further nesting activity at this burrow. Female possibly nested away from own burrow.	1*		
Resident 3	2 June 2013, 1154–1159: Abandoned nesting attempt at own burrow when male visited. 4 June 2013, 1047–1240: Nested at own burrow.		2	1
Resident 4	9 June 2013, 1011: Left own burrow. Tracked to new burrow at 1850 h. Apron of new burrow contained fresh nest.	1*	1	
Resident 6	5 June 2013, 1011–1103: Nested at own burrow. Visiting male disrupted nest manicuring activity.		2	1
Resident 8	9 June 2013, 1447–1615: Nested at own burrow.		6	
Resident 9	7 June 2013, 1344–1441: Nested at own burrow.			
Visitor 1	25 May 2013, 1418–1428: Visited male-occupied burrow. Started to nest, but abandoned attempt.	1		1
Visitor 2	1 June 2013, 1425–1432: Visited Resident Female 8's burrow while resident was away. Started nesting, but abandoned attempt.	1	2	
Visitor 3	12 June 2013, 1736-1739: Visited Resident Female 2's burrow. Abandoned nesting attempt when resident emerged from burrow. Both tortoises abandoned burrow. 13 June 2013, 1440–1545: Returned and nested at vacant burrow.	2	1	1

Bonferroni-corrected Mann-Whitney U tests. We conducted statistical analyses in SPSS version 24.0 (IBM Corp. Released 2015. IBM SPSS Statistics for Mac, Version 24.0.) with $\alpha = 0.05$.

We describe encounters between nesting tortoises and conspecifics. We also characterized encounters between females and conspecifics outside of obvious nesting activity, but during the nesting season. To characterize interactions between females, we determined the proportion of female-female encounters (multiple individuals visible at the same time on video) that included at least one female responding aggressively to the other. We evaluated aggression at two levels. We considered an interaction to be aggressive if at least one female rammed the other. We considered the interaction potentially aggressive if one female blocked the burrow entrance. We used the same approach to describe encounters between females and large juveniles.

To characterize female-male interactions, we determined the proportion of female-male encounters in which the male attempted to mate with the female. We identified male mating behavior to include head bobbing or mounting attempts. We also calculated the proportion of female-male encounters and mounts that represented potentially successful mating attempts. Potentially successful matings appeared to be distinct from other mating attempts in that males remained mounted longer, made deep head thrusts, and dismounted females voluntarily (Supplemental Video 1). Males left female burrow areas immediately after potentially successful mating attempts. We did not assess aggression between females and males because subtle aggression is difficult to distinguish from mating activity.

Results

Summary of nesting observations.—Cameras documented six complete and six abandoned nesting attempts on Wade Tract by six resident and three visiting females (n = 9), all commencing between 1009–1736 on 25 May to 13 June 2013 (Table 1). Additionally, while conducting fieldwork, we observed a tenth female digging a nest cavity on a burrow apron outside of Wade Tract, but still on Arcadia Plantation in the late afternoon of 5 June 2013. She abandoned the attempt before ovipositing, but a nest was laid in the same location 2 d later. We found no indication of tortoises laying eggs more than once during the nesting season. All observed nesting attempts occurred on burrow aprons, approximately even with to three adult tortoise body lengths from the back edges of burrow entrances.

Table 2. Time spent by female Gopher Tortoises (*Gopherus polyphemus*) from a site in southwestern Georgia, USA, in each nesting stage and total time required to construct a nest (excluding nest manicuring activity). Different letters next to mean values denote significantly different time spent in stages (Bonferroni-corrected Mann-Whitney U tests, $P < 0.05$). Manicuring activity refers to manicuring activity on the day of oviposition and does not include additional nest manicuring on subsequent days.

Activity	Mean (min)	Range (min)	n
Circling/Digging Depression	7.0 (a)	0.0–15.0	8
Digging Egg Cavity	40.3 (b)	25.3–59.5	6
Oviposition	10.9 (a)	7.2–16.1	6
Covering Egg Cavity	15.3 (a)	10.0–22.0	6
Total Time to Construct Nest	73.8	52.1–112.6	6
Nest Manicuring	150.5 (c)	101.8–207.5	6

Tortoises did not limit nesting activity to their own burrows. Three visiting females attempted to nest (three observations) or nested (one observation: after the resident female left) at burrows of video-recorded conspecifics (Table 1). Resident females also may have nested at other burrows. One resident female left her burrow at 1011 on 9 June and was found at 1850 inside another burrow containing a freshly laid nest in the apron (Table 1). A second video-recorded resident female abandoned a nesting attempt at her burrow after hitting a large root, and, based on subsequent camera observations at her burrow, likely nested elsewhere. A third video-recorded resident tortoise that nested at her burrow had only moved to that burrow within the previous 10 d.

We documented seven females each abandon a single nesting attempt prior to oviposition, one for an unknown reason, one perhaps in response to an approaching rainstorm, and the remainder apparently in response to a root in the nest cavity (one female), researcher disturbance (one female), and conspecifics (three females; Table 1). Conspecifics also temporarily disrupted the nesting activities (nest covering and manicuring) of two females that had oviposited earlier in the day (Table 1).

Nesting behavior.—Nesting could be divided into five stages: circling and/or digging a shallow depression, digging the egg cavity, ovipositing, covering the nest, and manicuring the nest area. Time spent in different stages differed ($H = 25.8$, df = 4, $P < 0.001$; Table 2). Females exhibited wide variation in the first nesting stage, circling and/or digging a shallow depression, and not all females performed this stage. Four females initiated nesting by circling on their center axis at the prospective nest location. Four other tortoises initiated nesting by both circling and constructing a shallow depression (Suppl. Video 2). However, one of these tortoises started one nesting attempt by circling and digging a shallow depression, but started another by immediately excavating a nest cavity. Similarly, a ninth tortoise basked on her burrow apron for 29 min without changing position and transitioned directly to excavating a nest cavity in the same location without first circling or digging a shallow depression (Supplemental Video 3). Most females lowered their head to the ground a small number of times before nesting, but this behavior was minimal during this stage. Mean time spent circling and/or digging a shallow depression was 7.0 min (range = 0.0–15.0 min, n = 8: one female excluded because she abandoned her attempt during this stage; Table 2).

When excavating nest cavities, females faced away from, rather than toward, burrow entrances more often than expected by chance (nine of nine facing away; binomial test: $P = 0.004$) and used their hindlimbs to remove soil (Supplemental Video 4). As time progressed, individuals lifted up slightly on their forelimbs as if to reach deeper into the cavity with the hindlimbs. In some instances, females kicked excavated soil into and behind burrow entrances. Mean time to excavate the nest cavity was 40.3 min (range = 25.3–59.5 min, n = 6).

After constructing a nest cavity, tortoises oviposited immediately. All females laid eggs without interruption while facing away from the burrow entrance. Ovipositing females pumped their heads in and out of their shells (Supplemental Video 5). Due to tortoise and camera positioning, it was only possible to see into the egg chamber during one oviposition event. In that instance, the female used a hindlimb multiple times to manipulate eggs within the nest cavity. Two ovipositing females exhibited extensive frothy saliva or mucus discharge from the mouth and nares (Supplemental Video 6). One of these females also had discharge from the eyes. Mean time to oviposit was 10.9 min (range = 7.2–16.1 min, n = 6; Table 2).

After ovipositing, females immediately covered nests. Females initially used their hindlimbs to cover the eggs, while continuing to face away from the burrow entrance. Forelimbs remained planted stationary on the ground from when tortoises initiated cavity excavation until individuals nearly completed covering the nest using their hindlimbs, at which point the forelimbs were employed to finish the task (Supplemental Video 7). Mean time to cover nests was 15.3 min (range = 10.0–22.0 min, n = 6). Initiation of nesting through final covering of eggs averaged 73.8 min (range = 52.1–112.6 min, n = 6; Table 2).

After covering nests, females (n = 6) extensively manicured the nest area, burrow entrance, and surrounding burrow apron (Supplemental Video 8). Manicuring females kicked soil and other materials out of burrow entrances, some of which had accumulated

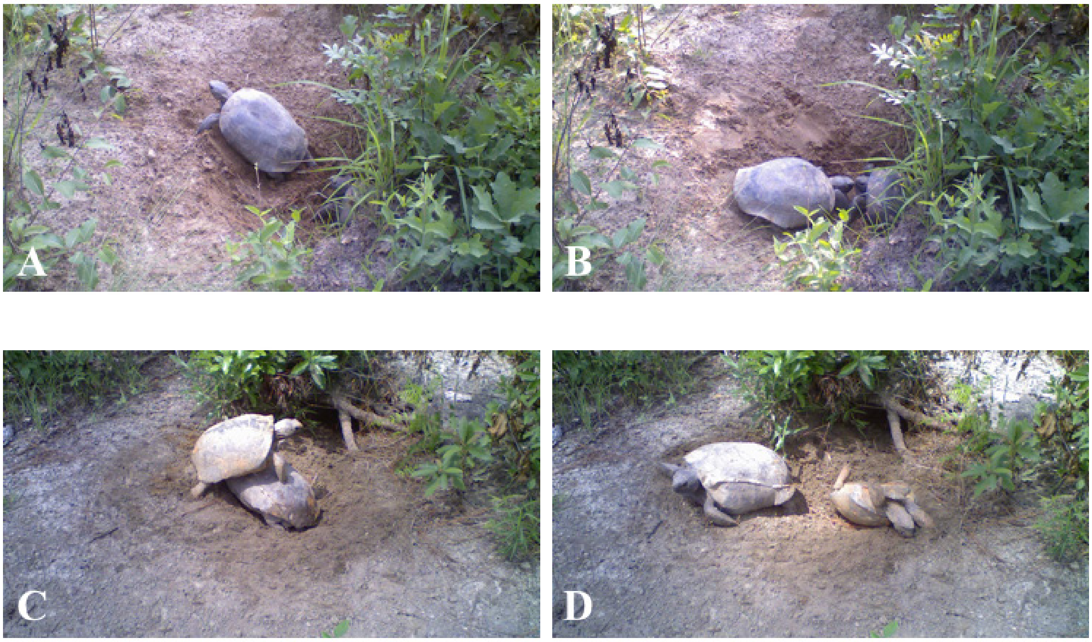

Figure 1. Images from time-lapse video camera stations at two Gopher Tortoise (*Gopherus polyphemus*) burrows in southwestern Georgia, USA. (A-B; Supplemental Video 10) Female Gopher Tortoise (Visitor 3; left) visits the apron of a burrow containing a female conspecific (Resident Female 2; right) and starts to excavate a nest cavity. Shortly thereafter, the resident female emerges; the visitor stops digging; the tortoises interact; and the visitor leaves. Later that day, the resident female also left. On the following day, the visiting tortoise returned and successfully nested at the vacant burrow. (C-D; Supplemental Video 11) Visiting male aggressively mounting a female (Resident Female 1) while she attempts to cover or manicure her nest, which she laid minutes before. The male overturned while attempting to mount the female.

during excavation of the nest cavity, and roughed up soil on the burrow apron using their forelimb claws. On average, females repeated the behavior of entering (or partially entering) burrows and kicking soil out 19.7 times (range = 11–30, n = 6 tortoises) and spent about 150.5 min (range = 101.8–207.5 min, n = 6; Table 2) engaged in manicuring activity during daylight hours following nesting. Manicuring females also repeatedly nuzzled the ground (Supplemental Video 8). On average individuals lowered their noses toward the ground at least 106 times (range = 22–200, n = 6) during manicuring activities before retreating into burrows by dark. Due to camera angles, vegetation, and low video frame rate (0.2 frames/ s), we likely undercounted this behavior. At least four of six females emerged from burrows much earlier than usual the morning following nesting and continued some manicuring activities. Observations on days following nesting were unavailable for two females. In one case, we installed protective wire mesh over the nest (Radzio et al. 2017) soon after it was laid, and the female left shortly thereafter and did not return. In the other case, the female overnighted in the burrow after nesting, but additional video was not recorded at that burrow.

Conspecific interactions during nesting.—We documented interactions between nesting females and conspecifics in five of 12 video-recorded nesting attempts (n = 6 total interactions, one nesting event included two interactions). In each instance that the interaction occurred before eggs were laid (n = 3), the female abandoned the nesting attempt (Table 1). In one interaction, a visiting female (Visitor 1) arrived at a burrow containing a male and immediately began to nest on the burrow apron, but abandoned the attempt soon thereafter, apparently when the male emerged (Table 1). Similarly, another female (Resident 3) immediately abandoned nest site preparation at her burrow when a male visited (Supplemental Video 9). She nested in the same location alone 2 d later. A third female (Visitor 3) visited a burrow containing another female and started to dig a cavity, but abandoned the attempt when the resident emerged (Fig. 1A–B; Supplemental Video 10). The two tortoises interacted on the burrow apron before both left the area. On the following day, when the burrow was vacant, the visiting female returned and nested. Visiting males disturbed two other females after they oviposited. A male visited a female (Resident 1) as she covered her nest and vigorously tried to mate with her, immediately biting, mounting, and ejaculating/ urinating on her shell. She was unreceptive, and at one point, the aggressive male overturned in the partially filled in nest (Supplemental Video 11; Fig. 1C–D). Later that day, another male visited, and disrupted nest

Table 3. Conspecific encounters (multiple individuals observed together) of Gopher Tortoises (*Gopherus polyphemus*) from a site in southwestern Georgia, USA, outside obvious nesting activity, but during the nesting season. Number of encounters (NE), encounters with interactions (EI), interactions with aggression (IA), interactions with mating attempts (IMA), and interactions with potential matings (IPM; interaction types defined in Materials and Methods). In six of 11 female-female interactions, at least one female rammed the other. In each of the five remaining potentially aggressive interactions, a female blocked the burrow entrance.

Encounter Type	NE	EI	IA	IMA	IPM
Female-Female	11	11	6–11	–	–
Female-Male	40	39	–	38	5
Female-Large Juvenile	3	3	2	–	–

manicuring activity, but may have successfully mated with the now more receptive female (Supplemental Video 1). A male also visited another female (Resident 6) as she manicured a nest she laid earlier in the day and distracted her from this activity for about 30 min (Supplemental Video 12; Table 1).

Additional female-female interactions at burrows.—Cameras documented 12 visits by females to female-occupied burrows outside obvious nesting activity (Table 3). Observations involved at least seven females. Visiting and resident females interacted in 11 of 12 visits (Table 3). In the lone visit without an interaction, the resident tortoise remained inside the burrow out of camera view while the visitor briefly inspected the burrow entrance. Ten of the 11 interactions involved at least one gravid tortoise (Table 1). Ten interactions lasted fewer than 20 min. One interaction, which included overt aggression, involved tortoises sharing a burrow for at least 2 d.

Six of 11 interactions involved overt aggression in which at least one female rammed the other tortoise with her the gular protrusion and/or carapace (Supplemental Video 13). At least five females exhibited such overt aggression toward another female. In three of the five remaining interactions without overt aggression, a female was initially at the surface and positioned itself (in two instances quite quickly) in the burrow entrance as if to prevent the other female from entering. In the remaining two interactions without overt aggression, a female was already in the burrow entrance, facing inside, and responded to another female on the burrow apron either by turning sideways in the burrow entrance or turning to face completely outward.

Additional female-male interactions at burrows.—Cameras documented 49 visits by males to females (n = 10) at their burrows outside of obvious nesting activity. A female (n = 9) was at, or emerged to, the surface during 40 of these visits. Males attempted to mate with females in at least 38 of 40 (95.0%) such encounters (Table 3).

Mating attempts often proceeded by: 1) the male headbobbing toward (and sometimes biting) the female; 2) the male backing away from a female; 3) if receptive, the female advancing toward the male; 4) the male continuing to headbob toward (and sometimes biting) the female; 5) the female turning around to face away from the male (and toward the burrow entrance); 6) the male rapidly mounting the female; 7) the female moving toward and into the burrow, which would cause the male to become dislodged or voluntarily dismount before copulating; and 8) often repeats of this sequence once the female reemerged from the burrow (Supplemental video 12). At other times, males initiated mating attempts by immediately mounting and, sometimes, biting females. Males regularly mounted females from ineffective copulatory positions, such as from the front or side of the carapace (Supplemental Video 11). Rapid mounting often led to ejaculation or urination onto female carapaces or onto the ground (Supplemental Video 11). In at least one instance, a male ejaculated or urinated onto the ground very soon after arriving, before even mounting the female.

Males mounted females as many as six times per interaction with obvious mating attempt (mean = 1.8 mounts), but appeared to copulate only in up to five of 69 (7.2%) total mounting attempts, or five of 38 (13.2%) interactions involving obvious mating attempts (Table 3). In these potentially successful copulations, which were distributed evenly among five females, males remained mounted longer, made deep head thrusts, dismounted females voluntarily, and left immediately thereafter (Supplemental Video 1). Similar to ovipositing females, several males expelled mucus or saliva from their nares during potentially successful copulation events. Although male mating attempts often were aggressive, we did not observe females exhibiting overt aggression (i.e., ramming, pushing) toward males.

Female-large juvenile interactions at burrows.—Large juveniles (about 15 cm carapace length) briefly visited burrows containing adult females on five occasions. On two occasions, the resident female emerged from the burrow and rammed the smaller tortoise (Supplemental Videos 14 and 15). On one occasion, a large juvenile visited a burrow while the resident female was inside and a visiting female was about to initiate a nesting attempt on the burrow apron. The large juvenile and the visitor interacted, but the interaction did not include overt aggression (Supplemental Video 16). On two other occasions, large juveniles visited burrows containing adults, but the adult did not emerge from the burrow nor was observed in the entrance (Table 3).

Discussion

Nesting behavior.—Similar to reports for other Gopher Tortoise populations (Landers et al. 1980; Butler and Hull 1996; Epperson and Heise 2003; Hammond 2009; Lamb et al. 2013), females at this site frequently, perhaps predominantly, nest at burrow aprons. Gopher Tortoises in Georgia nest up to once annually (Landers et al. 1980), and at least 6–7 of 10 resident females in this study exhibited nesting activity at burrow aprons. We also add to other reports suggesting that females do not nest exclusively at their burrow aprons but may select nest sites from among multiple burrows, including those of juvenile tortoises, and other bare ground areas (Landers et al. 1980; Lamb et al. 2013; Radzio et al. 2017). Our observations suggest that at least five females exhibited nesting activity away from their burrows, one on two occasions (Table 1). Additionally, another tortoise that nested at her burrow had only moved to that burrow within the previous 10 d. Although quantitative data are limited, tortoises may select among multiple potential nest sites on the basis of vegetative cover, soil composition, and thermal environment (Landers et al. 1980; Diemer and Moore 1993; Smith 1995; Lamb et al. 2013).

In some diurnal turtle species, high daytime temperatures constrain nesting to night hours and other cooler times of day (Spotila and Standora 1985). Video-recorded nesting observations distributed rather uniformly between 1000 and 1800, but sample sizes were low. However, cameras did not monitor possible night activity. Given that females required on average more than an hour to nest, and that in hot environments body temperatures of adult Gopher Tortoises can increase from typical active values (mean = 34.7° C) to temperatures at which individuals begin to froth (≥ 38.0° C) in as little as 10 min (Douglass and Layne 1978), females should avoid nesting in open habitats during hot weather. In this study, two video-recorded females secreted large amounts of mucus or frothy saliva when thrusting their heads in and out of shells during oviposition. Although it is possible that this discharge represented a physiological response to thermal stress (Douglass and Layne 1978; Johnston 1996), we were unable to unambiguously assess heat loads experienced by these nesting tortoises. Additionally, discharge may have reflected symptoms of upper respiratory disease (McLaughlin et al. 2000) or simply represented a feature of nesting that sometimes occurs in healthy individuals of this species when they thrust their heads deeply in and out of their shell during oviposition. Notably, some males exhibited similar discharge when performing deep head thrusts during potentially successful mating attempts.

Gopher Tortoises in this study exhibited many typical turtle nesting behaviors, including nest site preparation (Ehrenfeld 1979), but this activity was plastic even within individuals. Kenefick (1954) reported that a captive Gopher Tortoise began nesting by swinging its body in a circle and digging a shallow depression with its forelimbs. We observed similar behavior in most nesting tortoises, but several times females started nesting by immediately digging an egg cavity with their hindlimbs. Females engaged in little to no ground-nuzzling behavior before starting to nest (Morjan and Venlenzuela 2001 and references therein), but as described below, engaged in this behavior extensively when manicuring the nest area following oviposition. Typical of most chelonians (but see Kuchling 1993), individuals in this study used their hindlimbs to both excavate and initially cover the egg cavity (Ehrenfeld 1979). Tortoises required considerable time to excavate the nest cavity, but after doing so, immediately laid eggs, on average within 11 min. By ovipositing quickly and immediately covering the nest, tortoises may reduce depredation risk to themselves and their eggs and also prevent nest substrate from losing excessive moisture. Unlike as reported for captive Agassiz's Desert Tortoises (*Gopherus agassizi*; Lee 1963) and free-ranging Texas Tortoises (*G. berlandieri*; Auffenberg and Weaver 1969; Rose and Judd 2014), we did not observe Gopher Tortoises urinating on nests. However, due to camera angles and tortoise orientations, we could only see into the nest cavity in one video.

Tortoises always oriented facing away from burrow entrances while excavating the nest cavity (Butler and Hull 1996), ovipositing, and covering eggs. The soil in front of burrows often slopes down toward the burrow entrance (Thomas Radzio, pers. obs.). Facing upslope may allow females to reach deeper into the nest cavity with their hindlimbs, deposit excavated soil downhill, and detect potential predators (Butler and Hull 1996) or visiting conspecifics more easily because the head remains elevated and out of the burrow. This orientation often also results in excavated soil being scattered behind the back edge of the burrow entrance, a sign that can be used by investigators to locate nests (Matt Hinderliter, pers. comm.).

After covering nests, females manicured nest areas, perhaps having the effect of reducing egg depredation, which can be very high in Gopher Tortoise populations (Landers et al. 1980; Smith et al. 2013). Kenefick (1954) reported that after covering her nest, a captive Gopher Tortoise "walked back and forth over the nest area and brushed it lightly with the nails of her front feet" for a short period. Our observations indicate that wild females engage in extensive nest manicuring intermittently throughout the day, or even days, following nesting and suggest that females also disguise nests by kicking soil out of burrows onto burrow aprons. All females intermittently kicked soil out of the burrow and onto the apron throughout the afternoon following nesting. Using their forelimbs, they also roughed up soil over a portion of the burrow apron. By excavating soil from burrows, tortoises can remove material that accumulated in burrow entrances during nest cavity excavation and create the visual appearance of a burrow that has been dug out or cleaned by a tortoise, rather than one that contains a nest in its apron. It is also possible that by kicking soil out of burrows, which frequently contain tortoise feces, tortoises mix in odors from the burrow to the nest area, and that this may confuse potential predators that locate turtle nests via olfactory cues, including volatiles released from disinterred soils (Buzuleciu et al. 2016). Manicuring females engaged in extensive ground nuzzling, a common turtle nesting behavior hypothesized to play a role in nest site selection either via detection of thermal or olfactory cues (Morjan and Valenzuela 2001). Therefore, it is notable that Gopher Tortoises ground nuzzled extensively after, but very little or not at all before nesting. A recent study of Painted Turtles (*Chrysemys picta*) suggests females can detect nests of conspecifics via olfactory cues (Iverson et al. 2016), and we speculate that Gopher Tortoises use ground nuzzling behavior and olfactory senses to guide efforts to disguise nest odors. Disguising nest odors for even a few days may be highly beneficial because turtle nests may be at greatest risk of depredation early in incubation (Congdon et al. 1983, 1987). Interestingly, a camera documented a Gray Fox (*Urocyon cinereoargenteus*) visit a burrow apron containing a nest that had been laid fewer than 6 h earlier. The female, who was sitting atop her nest when the fox arrived, quickly hid inside. The fox left the burrow seconds later without disturbing the nest. Although not observed in this study, recent accounts suggest that some female Gopher Tortoises defend nests against potential predators (Grosse et al. 2012; Dziadzio and Smith 2015). Nest defense is also documented in several western *Gopherus* species, including ones that often nest inside burrows (Roberson et al. 1985; Turner et al. 1986; Agha et al. 2013 and references therein), where predation risk to defending females might be limited because large predators cannot enter narrow burrows.

Conspecific interactions.—Our observations suggest that, in addition to abiotic factors (Landers et al. 1980; Diemer and Moore 1993; Smith 1995; Lamb et al. 2013), conspecific interactions may directly or indirectly influence where individual females nest. In our study population, approximately one-quarter to one-half of adult-sized tortoise burrows are used by an adult tortoise at any given time (Burke 1989; Guyer et al. 2012), and tortoises spend virtually all of their nighttime hours and nearly all of their daytime hours at burrows (unpubl. data). In each of the three instances where we documented a female attempting to nest in the presence of a conspecific, the female abandoned the attempt. It is likely more difficult for a female to nest at a burrow occupied by an adult conspecific because as our observations of tortoise interactions indicate, if the burrow contains a female, she may be may be aggressively pushed or rammed, or if it is occupied by a male, she may be aggressively bit and/or mounted (Douglass 1986; Johnson et al. 2007; Guyer et al. 2014; this study). Even if she manages to oviposit, her eggs could be inadvertently trampled and broken during interactions with the conspecific. Any of these possibilities could explain why females abandoned nesting attempts following interactions with conspecifics.

To adversely influence reproductive success or offspring phenotype, conspecific constraints on nesting activity must affect nest characteristics such as depredation risk or incubation conditions. Although Gopher Tortoise nests at our site exhibit substantial variation in hatching success (0–100%) and oviposition-to-hatchling emergence times (96–128 d; Radzio et al. 2017), potentially reflecting underlying variation in incubation conditions, our data do not assess whether social interactions affect reproductive outcomes. However, our observations do suggest that, if Gopher Tortoises exhibit nest site philopatry, it could be somewhat obscured by conspecific constraints on where females nest.

We document apparent burrow competition involving gravid female tortoises, avoidance responses by nesting females to male and female conspecifics, and other social interactions outside of nesting in an old-growth Longleaf Pine forest that suggest movements and nest-site choices of female Gopher Tortoises may be influenced by conspecific interactions. Old-growth Longleaf Pine forest is hypothesized to be one of the primary ancestral habitats of Gopher Tortoises (Guyer and Herman 1997), but Gopher Tortoises inhabit a variety of environments, including less productive Longleaf Pine ecosystems and barrier islands where ground cover is less dense. At a site characterized by many unvegetated areas, Smith (1995) documented extensive nesting activity by Gopher Tortoises away from, but very little at, burrow aprons. Therefore, our observations may serve as a reference for how social interactions influence the nesting ecology of Gopher Tortoises in a portion of their natural environment, particularly where tortoises occur in high densities and nest extensively on burrow aprons.

Acknowledgments.—We thank Jaci Smolinsky and Brent Mills for valuable assistance in the field. Tim Mok helped process the video data. Maryann Fitzpatrick and Wolfgang Nadler graciously shared their expertise on a variety of technical topics. This work was funded by a graduate teaching assistantship and a McLean Fellowship in Ornithology and Environmental Science from the Department of Biodiversity, Earth, and Environmental Science at Drexel University. The Wade Tract Research Fund, Chicago Herpetological Society, Minnesota Herpetological Society, Western Digital Foundation, Biology Department at Drexel University, National Aeronautical and Space Administration, and Betz Chair Endowment in Environmental Science at Drexel University provided funding and/or equipment used in this study. We thank Paddy Wade, the Wade Family, and the entire staff of Arcadia Plantation, including Paul Massey, for allowing access to their property and for their ongoing support of research at the site. This work was conducted in accordance with the Drexel University Institutional Animal Care and Use Committee (protocol number: 19661) and the Georgia Department of Natural Resources (permit number: 24821).

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