Notes

Recommendation for Gopher Tortoise Burrow Buffer to Avoid Collapse from Heavy Equipment

Lora L. Smith,* Matt Hinderliter, R. Scott Taylor, Jennifer M. Howze

L.L. Smith, R.S. Taylor, J.M. Howze
Joseph W. Jones Ecological Research Center, 3988 Jones Center Drive, Newton, Georgia 39870

M. Hinderliter
U.S. Fish and Wildlife Service, 6578 Dogwood View Parkway, Jackson, Mississippi 39213

Abstract

Gopher tortoises (*Gopherus polyphemus*) occur in open-canopy pine habitat on well-drained soils in the southeastern United States, where they construct burrows that offer protection from thermal extremes, fire, and predators. Gopher tortoise populations have declined over the past 50 y, primarily as a result of habitat loss and degradation. Southeastern pine forests require active management with prescribed fire, mechanical thinning, or removal of hardwoods to maintain suitable habitat for gopher tortoises. In addition, many pine forests in the Southeast that support gopher tortoise populations are managed for multiple uses including intensive silviculture. Heavy equipment associated with these activities used in proximity to gopher tortoise burrows can cause them to collapse, potentially causing harm to tortoises or other imperiled organisms that use their burrows. Hence, there is a need for practical guidelines for use of heavy equipment for timber harvest, management, and other activities around gopher tortoise burrows to minimize risk to tortoises. We conducted a field study to determine the distance at which heavy equipment caused gopher tortoise burrows to collapse using a feller buncher, rubber-tire front-end loader, and an agricultural tractor with a tree-mower attachment in sandy clay loam (15 burrows) and undifferentiated deep sand (15 burrows) soils at a site in southwestern Georgia. All burrows were confirmed to be unoccupied by tortoises or other vertebrate commensal species using a camera scope before collapse. The greatest mean distance to collapse across all vehicles tested in sandy clay loam and undifferentiated deep sand was 2.19 $\pm$ 0.56 m and the maximum distance to collapse was 3 m. Given the variation in collapse distance, we recommend a buffer that extends 4 m in radius from the entrance of the gopher tortoise burrow to minimize risk of collapse from heavy equipment.

Keywords: reptile; gopher tortoise; burrow; heavy equipment; management

Received: June 30, 2015; Accepted: September 10, 2015; Published Online Early: September 2015; Published: December 2015

Citation: Smith LL, Hinderliter M, Taylor RS, Howze JM. 2015. Recommendation for gopher tortoise burrow buffer to avoid collapse from heavy equipment. *Journal of Fish and Wildlife Management* 6(2):456–463; e1944-687X. doi: 10.3996/062015-JFWM-055

* Corresponding author: lora.smith@jonesctr.org

Introduction

The gopher tortoise (*Gopherus polyphemus*) is a long-lived reptile native to the fire-maintained open-canopied pine forests that occur on well-drained soils in the southeastern United States. Gopher tortoises construct extensive burrows that offer protection from fire, thermal extremes, and predators (Figure 1; Ashton and Ashton 2008), and gopher tortoise burrows provide shelter for more than 360 other species including at least 60 vertebrates and 302 invertebrates (Jackson and Milstrey 1989; Lago 1991). Tortoise burrows vary in length and depth depending on soil characteristics and depth to the water table, but average 4.6 m in length and 1.8 m in depth (Cox et al. 1987); however, in excessively well-drained soils, burrows as long as 20.4 m have been

Figure 1. Gopher tortoise (*Gopherus polyphemus*) at the entrance of a burrow.

reported (Ashton and Ashton 2008). Gopher tortoises generally forage in proximity to their burrow and females often deposit nests in the mound of sand at the burrow entrance in late spring and early summer (Eubanks et al. 2003; Ashton and Ashton 2008). In gopher tortoise populations within fire-maintained, open longleaf pine (*Pinus palustris*) habitat, female tortoises use an average of 5 burrows per year, whereas males use an average of 10 burrows per year (McRae et al. 1981; Diemer 1992; Smith 1995; Tuma 1996; Boglioli et al. 2000; Eubanks et al. 2003). Thus, there are often numerous unoccupied tortoise burrows within a population at any given time. These burrows, though unoccupied by gopher tortoises, may be occupied by commensals.

Gopher tortoise populations have declined precipitously over the past 50 y, primarily as a result of habitat loss and degradation (Auffenberg and Franz 1982). Longleaf pine forests of the southeastern United States require active management to maintain the open-canopied condition with abundant herbaceous ground cover that gopher tortoises and many other longleaf pine specialists require (DeBerry and Pashley 2004). The suppression of wildfires that would have historically been the primary means of natural forest disturbance and maintenance results in encroachment of hardwood shrubs and trees (oaks, *Quercus* spp., in particular), and ultimately to a closed-canopied forest (Gilliam and Platt 1999; Knapp et al. 2009). Despite the current use of prescribed fire to manage many southeastern pine forests, constraints on use of fire in certain situations have resulted in a decline in high-quality tortoise habitat even on protected areas (Haines et al. 2001; Hermann et al. 2002; McCoy et al. 2006). Successional changes in overstory vegetation that lead to canopy closure accelerate burrow abandonment by gopher tortoises (Aresco and Guyer 1999; Jones and Dorr 2004; Yager et al. 2007).

In many cases, forestry management practices such as mechanical thinning and hardwood removal benefit gopher tortoises by restoring a more open canopy and encouraging growth of herbaceous food plants (Jones and Dorr 2004). However, heavy equipment associated with these activities used in proximity to burrows can result in death or injury to tortoises, entrapment of tortoises within their collapsed burrows, and damage to burrows or nests (Landers and Buckner 1981; Diemer and Moler 1982; Diemer 1992; Epperson 1997). Collapse of burrows from heavy equipment can also cause death, injury, and entrapment of commensals, some of which are even more imperiled than the gopher tortoise, for

example, the federally threatened eastern indigo snake (*Drymarchon couperi*; US Endangered Species Act [ESA 1973, as amended]; Stevenson 2010) and critically imperiled gopher tortoise acrolophis moth (*Acrolophis pholeter*), which is known from only one county in Florida (Jackson and Milstrey 1989; Nature Serve 2015). Much of the remaining tortoise habitat on private lands in the Southeast is managed for timber production (Zhao et al. 2013), which often involves silvicultural activities with heavy equipment. Military bases, which frequently support large numbers of gopher tortoises, are not only managed for timber production but also have military mission support and training activities that may include use of heavy equipment within tortoise habitat. Hence, there is a need for guidance for safe use of heavy equipment around tortoise burrows so that risk to tortoises and their burrows can be minimized while allowing habitat management flexibility to landowners and managers.

Despite concern about tortoise mortality from burrow collapse (Auffenberg and Franz 1982), there are numerous reports on the ability of gopher tortoises to self-excavate from collapsed burrows (Landers and Buckner 1981; Diemer and Moler 1982; Diemer 1992; Epperson 1997). Diemer and Moler (1982) and Landers and Buckner (1981) monitored tortoises after their burrows were collapsed from forestry activities and found that all of them ($n = 3$ and $n = 11$, respectively) self-excavated within 3 to 8 wk. Three studies specifically investigated the direct and indirect effects of burrow collapse on gopher tortoises. The first study, by Wester and Kolb (2008), investigated the self-excavation of adult and subadult gopher tortoises from intentionally collapsed burrows in different soil types. Tortoises took an average of 63.9 d ($n = 16$) to self-excavate in sandy soils, and an average of 35.6 d ($n = 14$) in clay soils (total range from both soil types was 2 to 107 d). However, one tortoise (in clay soils) failed to excavate after 107 d and was discovered dead in its burrow, apparently as a result of its burrow being collapsed. The second study by Mendonça et al. (2007) involved collapsing occupied gopher tortoise burrows using logging and military vehicles at Fort Benning, Georgia. Tortoises were monitored to assess whether they were injured or killed, the time to self-excavation, and the short-term physiological and behavioral effects of entrapment. A third study at Fort Benning included telemetry of tortoises whose burrows had not been collapsed, to compare long-term movements and behavior with the group of tortoises that had been entombed (Beauman 2008). No tortoises were killed or appeared physically harmed by the act of collapsing their burrows, and self-excavation occurred from several hours to 85 d after burrows were collapsed. Although none of the entombed tortoises were directly harmed, there was a high rate of burrow abandonment after self-excavation (Beauman 2008). Levels of corticosterone, a hormone associated with stress response, increased significantly with duration of entrapment and there was some evidence that entrapment and prolonged elevated corticosterone levels may have had a long-term effect on immune response (Mendonça et al. 2007).

In the western portion of the range of the gopher tortoise where the U.S. Fish and Wildlife Service (USFWS) has listed the gopher tortoise as a threatened species (U.S. Endangered Species Act [ESA] 1973, as amended; USFWS 1987), the destruction of a gopher tortoise burrow (even if it is unoccupied) may be considered likely to cause harm. By the USFWS's definition, harm "may include significant habitat modification or degradation when it actually kills or injures wildlife by significantly impairing essential behavioral patterns including breeding, feeding, or sheltering" (USFWS 1987). To avoid destruction of burrows, the practice of maintaining a buffer around known gopher tortoise burrows when using heavy equipment or machinery has been a part of military training policy recommendations, federal and state guidelines, research studies, and habitat management plans in several states, some for more than 20 y. For example, the Land and Resource Management Plan for National Forests in Florida (USDA-FS 1999) instructs all timber sale unit openings and maintenance management plans for new or renewed rights-of-way permits to have clearly marked 4.6-m buffers around the entrance to gopher tortoise burrows, and that heavy equipment should be kept out of this buffer zone. At Fort Benning, Georgia, gopher tortoise burrows identified as potentially being affected by off-road training with wheeled and tracked vehicles are marked with signs limiting vehicular traffic within 15.2 m of the burrows (IAW MCOE Regulation 350-19). Justification for these specific buffer widths was not provided, although the 4.6 m buffer may be based on a published account of average burrow length (Cox et al. 1987).

Measures for avoiding gopher tortoise burrows have been recommended for the protection of other at-risk species as well. This is of particular concern for species like the eastern indigo snake and Florida gopher frog (*Lithobates capito*), which may use unoccupied tortoise burrows. Without a tortoise to excavate a collapsed burrow, these species may become entombed. If the collapse occurs in winter, tortoises are not likely to self-excavate, and these two species could remain trapped in the burrow during their breeding season. Stevenson (2010) advised avoiding ground-disturbing activities (such as timber harvest and vehicle activity) within a 2-m buffer around tortoise burrows to prevent entombment of eastern indigo snakes. Several sources have identified 7.6 m as the minimum buffer distance to maintain around gopher tortoise burrows to prevent damage to the burrow (Wilson et al. 1997; 2014 USDA-FS Revised Land and Resource Management Plan for National Forests in Mississippi, Florida Department of Transportation– Listed Species Guidelines).

Although various buffer distances have been implemented in the past, to our knowledge the distance from a tortoise burrow entrance at which heavy equipment is likely to cause collapse has not been investigated. Because of the need to implement management activities to restore tortoise habitat range-wide, as well as concern by private landowners throughout the

Table 1. Approximate specifications for heavy equipment used in gopher tortoise (*Gopherus polyphemus*) burrow collapse study at Ichauway in Baker County, Georgia, 2013. Weight estimates were obtained from manufacturer web sites.

Heavy equipment	Vehicle width (m)	Weight (kg)
Agricultural tractor with tree mower	1.78	5,000
Rubber-tire front-end loader	2.30	10,000
Feller buncher	2.44	15,000

Southeast about potential restrictions on timber management activities, we conducted a field study to provide data for a recommended buffer width around tortoise burrows using unoccupied gopher tortoise burrows and common forestry equipment.

Methods

This study was conducted using unoccupied gopher tortoise burrows at Ichauway, the research site of the Joseph W. Jones Ecological Research Center in Baker County, Georgia in August 2013. We selected burrows of adult tortoises ($>$ 22 cm in width) in areas with undifferentiated deep sand (typic quartzipsamment; Lakeland and Bigbee series) and sandy clay loam (grossarenic kandiudult; Troup series) soils on the basis of Natural Resource Conservation Service soils maps. Soils in the vicinity of burrows were verified using a bucket auger, categorized by great group, and corroborated with soil maps drawn by an independently contracted soil scientist for a separate site-wide soil description project. To minimize potential impact to the tortoise population from collapsing burrows, we limited our sample to 30 unoccupied burrows. To confirm that they were unoccupied by tortoises or vertebrate commensal species, all burrows were searched with a burrow camera scope (Environmental Management Systems, Canton, GA) immediately preceding collapse trials. The length of each burrow was measured to the nearest 0.25 m using the camera scope, which consisted of a camera at one end of a 5-m-long hydraulic hose that housed the wiring to the battery and monitor. Thus, burrow length was the length of the hose plus the camera when the camera reached the back of the burrow. We flagged the approximate end of the burrows on the basis of the measured length as a visual cue for equipment operators.

We used three types of heavy equipment vehicles in this study: feller buncher, rubber-tire front-end loader, and an agricultural tractor with tree-mower attachment (see Table 1 for weight and width measurements). Each vehicle was driven across five different burrows in each of the two soil types (10 burrows per vehicle for a total of 30 burrows). Vehicles were driven at operational speeds across and approximately perpendicular to the burrow at increasingly closer distances to the burrow entrance (Figure 2). A pass across a burrow consisted of each pair of front and rear tires of the vehicle crossing the burrow four times. On the first pass, the inside wheels of the vehicle crossed the approximate end of the burrow. On the second pass, the inside wheel was placed one vehicle-width closer to the burrow entrance, with the outside tires placed in the track of the previous pass, and so on, until wheels approached to within 1–1.5 m of the burrow entrance. In some cases, we had to place the inside tires midway between the tracks of the previous path to make a final pass within 1–1.5 m from the entrance. The number of passes differed among burrows because of variation in the length of burrows. After each pass by a vehicle across a burrow, we rescoped the burrow to see if it had collapsed. If there was a collapse, we recorded the length along the burrow to the point of collapse to the nearest 0.25 m using the burrow camera cable. We also measured the distance from the inside tire of the vehicle to the burrow entrance if the burrow had collapsed and reported this as the "distance to collapse." We used an analysis of variance to determine if the mean distance to collapse differed by vehicle or soil type (sandy clay loam vs. undifferentiated deep sand). This analysis was run in Program R (R Core Team 2015); results were considered significant at $P < 0.10$.

Results

We tested a total of 30 burrows for collapse (15 in sandy clay loam and 15 in undifferentiated deep sand). The burrows varied considerably in length, from 2.5 to 6 m, but we were able to make at least two passes across each burrow with each vehicle (Table 2; Table S1, *Supplemental Material*). The three types of heavy equipment used in this study collapsed 26 of the 30 (87%) burrows tested. In almost all cases, if a burrow collapsed, soil from the collapse could be detected within 1–2 m of the burrow entrance. In the sandy clay loam, the farthest distance at which a vehicle collapsed a burrow was 2.25 m, whereas in the undifferentiated deep sand, the maximum distance to collapse was 3.0 m.

There was a significant interaction between equipment and soil type ($F_{1,2} = 3.588$, $P = 0.043$). Mean distance to collapse was greater for the front-end loader in undifferentiated deep sand than in sandy clay loam (2.19 ± 0.56 m as compared with 1.08 ± 0.64 m, respectively, $P = 0.091$; Figure 3). In undifferentiated deep sand, the average distance to collapse was greater for the front-end loader than for the tractor (2.19 ± 0.56 m as compared with 1.07 ± 0.62 m, respectively, $P = 0.088$; Figure 3).

The agricultural tractor had the shortest mean distance to collapse (1.08 ± 0.64 m in undifferentiated deep sand and 1.31 ± 0.78 m in sandy clay loam). However, the tractor collapsed one burrow in the sandy clay loam at 2.25 m from the entrance. The front-end loader had the greatest mean distance to collapse of all equipment tested at 2.19 ± 0.56 m in undifferentiated deep sand and one burrow in this soil type was collapsed at 3.0 m.

Discussion

The three types of heavy equipment tested in this study caused collapse of most gopher tortoise burrows

Figure 2. Rubber-tire front-end loader being driven across an unoccupied gopher tortoise (*Gopherus polyphemus*) burrow at Ichauway, Baker County, Georgia in 2013. The burrow entrance is marked with an orange flag.

(87%) when driven across the burrow within 3 m of the entrance. Distance to collapse with the front-end loader, which weighed approximately 10,000 kg, was greater in undifferentiated deep sand than in the sandy clay loam. The front-end loader also collapsed burrows from a greater distance than the agricultural tractor, the lightest vehicle tested (5,000 kg). The greatest distance to collapse with the feller buncher, the heaviest vehicle tested (15,000 kg), was 2 m. We suspect that differences in wheel base and tire surface area, rather than total

Table 2. Results of gopher tortoise (*Gopherus polyphemus*) burrow collapse study at Ichauway in Baker County, Georgia, 2013. The three types of heavy equipment used included an agricultural tractor with tree-mower attachment (Tractor), a rubber-tire front-end loader (FE loader), and a feller buncher (F buncher). All burrows were confirmed to be unoccupied by tortoises and vertebrate burrow associates before collapse. Lengths are reported in meters. SD = standard deviation.

Soil type	Equipment type	# Burrows	Burrow length	Max. distance to collapse	Mean distance to collapse (SD)	Burrow length to collapse	# Collapsed
Sandy clay loam							
	Tractor	5	3.25–5	2.25	1.31 (0.78)	0.5–1	4 of 5
	FE loader	5	3–6	2.0	1.08 (0.65)	1–2.25	4 of 5
	F buncher	5	3–4	1.5	1.50 (0.00)	1–1.25	5 of 5
Undifferentiated deep sand							
	Tractor	5	3.5–5.5	1.75	1.07 (0.62)	0.5–2	5 of 5
	FE loader	5	3.5–5.25	3.0	2.19 (0.56)	1–3	5 of 5
	F buncher	5	2.5–4	2.0	1.36 (0.73)	0.75–1	4 of 5

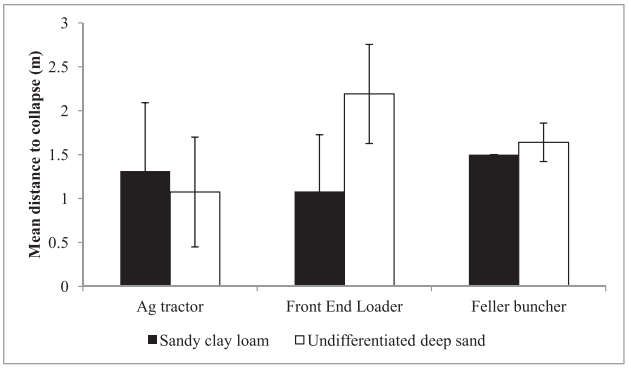

Figure 3. A comparison of mean distance to collapse by heavy equipment (feller buncher, rubber-tire front-end loader, and an agricultural tractor with tree-mower attachment) for unoccupied gopher tortoise (*Gopherus polyphemus*) burrows in sandy clay loam and undifferentiated deep sand at Ichauway, Baker County, Georgia in 2013. Error bars indicate 1 standard deviation (SD).

weight, among the vehicle types may explain differences in distance to collapse.

The greatest mean distance to collapse across all vehicles tested in undifferentiated deep sand and sandy clay loam was 2.19 ± 0.56 m and the maximum distance to collapse was 3 m. Given the variation in distance to collapse in this study, we recommend a buffer that extends 4 m in radius from the entrance of the gopher tortoise burrow to minimize risk of collapse from heavy equipment. We also recommend that burrows be conspicuously marked before heavy equipment use to ensure that equipment operators can identify burrows to maintain this buffer distance. Although our study was limited to adult-sized burrows, the buffer width recommendation is likely to also prevent collapse of burrows of juveniles and subadults; however, hatchling burrows and pallets would be difficult to detect and avoid (Ashton and Ashton 2008).

The dependence of the gopher tortoise on burrows located within open-canopy pine forests that require active management, either with prescribed fire or mechanical reduction of hardwoods, presents a potential for conflict between management and conservation. In addition, the occurrence of large, regionally significant tortoise populations on federal, state, and private lands with multiple land-use objectives provides a unique challenge and opportunity for conservation and management. At a population level, the benefits to gopher tortoises from activities that maintain or restore the open-canopy structure of pine forests (Jones and Dorr 2004; Tuberville et al. 2014) likely outweigh the risks to tortoises associated with occasional, unintentional collapse of individual burrows from use of heavy equipment. However, a research-based recommendation of a buffer to avoid impact to burrows is needed because minimizing risk of damage to gopher tortoise burrows will not only help protect resident tortoises and tortoise nests deposited at or near the entrance, but will also help protect other, potentially more imperiled species that use burrows.

Supplemental Material

Please note: The *Journal of Fish and Wildlife Management* is not responsible for the content or functionality of any supplemental material. Queries should be directed to the corresponding author for the article.

Table S1. Distance to collapse from heavy equipment data for gopher tortoise (*Gopherus polyphemus*) burrows at Ichauway in Baker County, Georgia, 2013. Burrows occurred in undifferentiated deep sand (Lakeland and Bigbee series) and sandy clay loam (Troup series) soils. An agricultural tractor, front-end loader, and feller buncher were driven across (perpendicular to) individual burrows (five per soil type) for up to four passes, depending on the length of the burrow. Equipment ran over each burrow four times with four tires unless otherwise noted. If burrow collapse was obvious, we only ran over a burrow twice.

Found at DOI: http://dx.doi.org/10.3996/062015-JFWM-055.S1 (14 KB XLSX)

Reference S1. Cox J, Inkley D, Kautz R. 1987. Ecology and habitat protection needs of gopher tortoise (*Gopherus polyphemus*) populations found on lands slated for large-scale development in Florida. Office of Environmental Service, Florida Game and Freshwater Fish Commission, Tallahassee, Florida.

Found at DOI: http://dx.doi.org/10.3996/062015-JFWM-055.S2 (8504 KB PDF)

Reference S2. DeBerry D, Pashley D. 2004. Pine ecosystem conservation handbook for the gopher tortoise. Washington, D.C.: American Forest Foundation.

Found at DOI: http://dx.doi.org/10.3996/062015-JFWM-055.S3 (1357 KB PDF).

Reference S3. Diemer JE. 1992. Home range and movements of the tortoise *Gopherus polyphemus* in northern Florida. Journal of Herpetology 26:158–165.

Found at DOI: http://dx.doi.org/10.3996/062015-JFWM-055.S4; also available at http://www.jstor.org/stable/1564857 (184 KB PDF).

Reference S4. Knapp EE, Estes BL, Skinner CN. 2009. Ecological effects of prescribed fire season: a literature review and synthesis for managers. Albany, California: USDA Forest Service, Pacific Southwest Research Station. PSW-GTR-224.

Found at DOI: http://dx.doi.org/10.3996/062015-JFWM-055.S5 (2685 KB PDF).

Reference S5. Mendonça MT, Beauman RL, Balbach H. 2007. Burrow collapse as a potential stressor on the gopher tortoise (*Gopherus polyphemus*). Final Report to the U.S Army Corps of Engineers, ERDC/CERL TR-07-33, Washington, D.C. 55pp.

Found at DOI: http://dx.doi.org/10.3996/062015-JFWM-055.S6 (2478 KB PDF).

Reference S6. Wilson DS, Mushinsky HR, Fischer RA. 1997. Species profile: Gopher tortoise (*Gopherus polyphemus*) on military installations in the southeastern

United States, Technical Report SERDP-97-10, U.S. Army Engineer Waterways Experiment Station, Vicksburg, Mississippi.

Found at DOI: http://dx.doi.org/10.3996/062015-JFWM-055.S7 (206 KB PDF).

Reference S7. Zhao S, Liu S, Sohl T, Young C, Werner J. 2013. Land use and carbon dynamics in the southeastern United States from 1992 to 2050. Environmental Research Letters 8 (2013): 044022.

Found at DOI: http://dx.doi.org/10.3996/062015-JFWM-055.S8 (3360 KB PDF).

Acknowledgments

Funding for this study was provided by the Georgia Department of Natural Resources. We thank Scott Smith, Michelina Dziadzio, Sonia Miller Smith, Jerry Wade, and Rex Hudgins for assistance with field data collection. C. Kenneth Dodd, John Jensen, the Associate Editor, and three anonymous reviewers provided comments that improved an earlier version of this manuscript. Liz Cox assisted with locating and formatting references.

Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

References

Aresco MJ, Guyer C. 1999. Burrow abandonment by gopher tortoises in slash pine plantations of the Conecuh National Forest. Journal of Wildlife Management 63(1): 26–35. Available: http://www.jstor.org/stable/3802484 (September 2015).

Ashton RE, Ashton PS. 2008. The natural history and management of the gopher tortoise. Malabar, Florida: Krieger Publishing.

Auffenberg W, Franz R. 1982. The status and distribution of the gopher tortoise (*Gopherus polyphemus*). Pages 95–126 in Bury RB, editor. North American Tortoises: conservation and ecology. Washington, D.C.: Wildlife Research Report No. 12.

Beauman RL. 2008. The effects of burrow collapse on the gopher tortoise (*Gopherus polyphemus*). Master's Thesis. Auburn, Alabama: Auburn University. Available: https://etd.auburn.edu/bitstream/handle/10415/1024/Beauman_Richard_19.pdf?sequence = 1 (September 2015).

Boglioli MD, Michener WK, Guyer C. 2000. Habitat selection and modification by the gopher tortoise, *Gopherus polyphemus*, in Georgia longleaf pine forest. Chelonian Conservation and Biology 3(4):699–705.

Cox J, Inkley D, Kautz R. 1987. Ecology and habitat protection needs of gopher tortoise (*Gopherus polyphemus*) populations found on lands slated for large-scale development in Florida. Office of Environmental Service, Florida Game and Freshwater Fish Commission, Tallahassee, Florida (see *Supplemental Material*, Reference S1, http://dx.doi.org/10.3996/062015-JFWM-055.S2).

DeBerry D, Pashley D. 2004. Pine ecosystem conservation handbook for the gopher tortoise. Washington, D.C.: American Forest Foundation (see *Supplemental Material*, Reference S2, http://dx.doi.org/10.3996/062015-JFWM-055.S3).

Diemer JE. 1992. Home range and movements of the tortoise *Gopherus polyphemus* in northern Florida. Journal of Herpetology 26:158–165. (see *Supplemental Material*, Reference S3, http://dx/doi.org/10.3996/062015-JFWM-055.S4); also available: http://www.jstor.org/stable/1564857 (September 2015).

Diemer JE, Moler PE. 1982. Gopher tortoise response to site preparation in northern Florida. Proceedings of the Southeastern Association of Fish and Wildlife Agencies. 36:634–637.

Epperson DM. 1997. Gopher tortoise (*Gopherus polyphemus*) populations, activity patterns, upper respiratory tract disease, and management on a military installation in northeast Florida. Master's thesis. Gainesville: University of Florida.

[ESA] U.S. Endangered Species Act of 1973, as amended, Pub. L. No. 93-205, 87 Stat. 884 (Dec. 28, 1973). Available: http://www.fws.gov/endangered/esa-library/pdf/ESAall.pdf (September 2015).

Eubanks JO, Michener WK, Guyer C. 2003. Patterns of movement and burrow use in a population of gopher tortoises (*Gopherus polyphemus*). Herpetologica 59(3): 311–321. Available: http://www.jstor.org/stable/3893608 (September 2015).

Florida Department of Transportation (2013, January 22). Listed Species Guidelines. Available: http://www.dot.state.fl.us/construction/DistrictOffices/d1web/Environmental/ListedSpeciesHome.shtm (September 2015).

Gilliam FS, Platt WJ. 1999. Effects of long-term fire exclusion on tree species composition and stand structure in an old-growth *Pinus palustris* (longleaf pine) forest. Plant Ecology 140:15–26. Available: http://link.springer.com/journal/11258 (September 2015).

Haines TK, Busby RL, Cleaves DA. 2001. Prescribed burning in the south: trends, purpose, and barriers. Southern Journal of Applied Forestry 25(4):149–153. Available: http://www.ingentaconnect.com/content/saf/sjaf/2001/00000025/00000004/art00001 (September 2015).

Hermann SM, Guyer C, Waddle JH, Nelms MG. 2002. Sampling on private property to evaluate population status and effects of land use practices on the gopher tortoise, *Gopherus polyphemus*. Biological Conservation 108:289–298. Available: http://www.sciencedirect.com/science/article/pii/S0006320702001234 (September 2015).

Jackson DR, Milstrey EG (1989). The fauna of gopher tortoise burrows. 1989. Proceedings of the Gopher Tortoise Relocation Symposium. Volume 86. State of Florida, Tallahassee, Florida: Game and Freshwater Fish Commission.

Jones JC, Dorr B. 2004. Habitat associations of gopher tortoise burrows on industrial timberlands. Wildlife

Society Bulletin 32(2):456–464. Available: http://www.jstor.org/stable/3784985 (September 2015).
Knapp EE, Estes BL, Skinner CN. 2009. Ecological effects of prescribed fire season: a literature review and synthesis for managers. Albany, California: USDA Forest Service, Pacific Southwest Research Station. PSW-GTR-224 (see *Supplemental Material*, Reference S4, http://dx.doi.org/10.3996/062015-JFWM-055.S5).
Lago PK. 1991. A survey of arthropods associated with gopher tortoise burrows in Mississippi. Entomology News 102:1–13.
Landers JL, Buckner JL. 1981. The gopher tortoise: effects of forest management and critical aspects of its ecology. Southlands Experimental Forestry Tech. Note 56.
McCoy ED, Mushinsky HR, Lindzey J. 2006. Declines of the gopher tortoise on protected lands. Biological Conservation 128(1):120–127. Available: http://www.sciencedirect.com/science/article/pii/S0006320705003824 (September 2015).
McRae WA, Landers JL, Garner JA. 1981. Movement patterns and home range of the gopher tortoise. American Midland Naturalist 1981:165–179. Available: http://www.jstor.org/stable/2425146 (September 2015).
Mendonça MT, Beauman RL, Balbach H. 2007. Burrow collapse as a potential stressor on the gopher tortoise (*Gopherus polyphemus*). Final Report to the U.S. Army Corps of Engineers, ERDC/CERL TR-07-33, Washington, D.C. (see *Supplemental Material,* Reference S5, http://dx.doi.org/10.3996/062015-JFWM-055.S6).
NatureServe. 2015. NatureServe Explorer: an online encyclopedia of life [web application]. Version 7.1. NatureServe, Arlington, Virginia. Available: http://explorer.natureserve.org. (September 2015).
R Core Team. 2015. R: a language and environment for statistical computing. Available: http://www. R-project.org. Vienna, Austria. (September 2015).
Smith LL. 1995. Nesting ecology, female home range and activity, and population size-class structure of the gopher tortoise, *Gopherus polyphemus*, on the Katharine Ordway Preserve, Putnam County, Florida. Bulletin of the Florida Museum of Natural History 37:97–126.
Stevenson DJ. 2010. Results of eastern indigo snake (*Drymarchon couperi*) surveys conducted at Okefenokee National Wildlife Refuge, Charlton County, Georgia. Project Orianne Ltd.
Tuberville TD, Todd BD, Hermann SM, Michener WK, Guyer C. 2014. Survival, demography, and growth of gopher tortoises (*Gopherus polyphemus*) from three study sites with different management histories. Journal of Wildlife Management 78(7):1151–1160. Available: http://onlinelibrary.wiley.com/doi/10.1002/jwmg.773/abstract (September 2015).
Tuma MW. 1996. Life history and population structure of the gopher tortoise on Camp Shelby, Mississippi. Mississippi Natural Heritage Program, Mississippi Museum of Natural Science. 1995 Yearly Report.
[USDA-FS] U.S. Department of Agriculture–Forest Service. 1999. Land and resource management plan for the National Forests in Florida. USDA-Forest Service, Tallahassee, Florida. Available: http://www.fs.usda.gov/detail/florida/landmanagement/?cid = stelprdb5269793 (September 2015).
[USFWS] U.S. Fish and Wildlife Service. 1987. Endangered and threatened wildlife and plants; determination of threatened status for the Gopher Tortoise (*Gopherus polyphemus*). Federal Register 52:12925376–25380.
Wester EE, Kolb JW. 2008. Impact of natural gas pipeline operation and maintenance on long-term population viability of the threatened gopher tortoise. Pages 499–511 in Goodrich-Mahoney JW, Abrahamson L, Ballard J, Tikalsky S, editors. Eighth International Symposium on Environmental Concerns in Rights-of-Way Management. New York: Elsevier. Available: http://www.sciencedirect.com/science/article/pii/B9780444532237500605 (September 2015).
Wilson DS, Mushinsky HR, Fischer RA. 1997. Species profile: gopher tortoise (*Gopherus polyphemus*) on military installations in the southeastern United States, Technical Report SERDP-97-10, U.S. Army Engineer Waterways Experiment Station, Vicksburg, Mississippi (see *Supplemental Material*, Reference S6, http://dx.doi.org/10.3996/062015-JFWM-055.S7).
Yager LY, Heise CD, Epperson DM, Hinderliter MG. 2007. Gopher tortoise response to habitat management by prescribed burning. Journal of Wildlife Management 71(2):428–434. Available: http://onlinelibrary.wiley.com/doi/10.2193/2006-337/abstract (September 2015).
Zhao S, Liu S, Sohl T, Young C, Werner J. 2013. Land use and carbon dynamics in the southeastern United States from 1992 to 2050. Environmental Research Letters 8 (2013):044022 (see *Supplemental Material*, Reference S7, http://dx.doi.org/10.3996/062015-JFWM-055.S8).