Gopher tortoise burrow surveys: External characteristics, burrow cameras, and truth

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Abstract. The gopher tortoise (*Gopherus polyphemus*) occupies the southeastern Coastal Plain of the United States where it digs burrows in upland habitats. Two burrow survey techniques commonly used to estimate tortoise population size (classification of burrows based on external characteristics and surveying burrow contents with a burrow camera) were tested to determine accuracy and subjectivity among researchers. Accuracy of both methods was verified by excavating the burrows to determine if tortoises were present. Classification of burrows based on external characteristics was found to be highly subjective, related to the researchers' prior gopher tortoise experience, and unrelated to familiarity with the landscape. Burrow camera surveys were accurate, but should be used with caution as mistakes can be costly. Inadequacies in the currently accepted burrow survey methods are discussed and suggestions for improvements are made.

Key words: Burrow classification; burrow occupancy; burrows; gopher tortoise; *Gopherus polyphemus*; protected species; surveying errors; survey methods.

Introduction

The gopher tortoise (*Gopherus polyphemus*) is a terrestrial reptile that digs its own burrows in a variety of upland habitats throughout the southeastern Coastal Plain of the United States. Population strongholds are in southern Georgia and the northern half of the Florida peninsula (Diemer, 1992), where they are protected by the states as threatened and a species of special concern, respectively. They are listed by the U.S. Fish and Wildlife Service as threatened west of the Tombigbee and Mobile

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Table 1. Categories and descriptions currently used for external characteristics classification of gopher tortoise burrows, based on Cox et al. (1987).

Burrow category	Description
Active	Obvious tracks or shell scraping signs at burrow mouth
Inactive	No tracks or shell scrapings; burrow occluded by debris, but recent use apparent
Abandoned	Burrow covered with sticks, weeds, grass; burrow collapsed, dilapidated

rivers in Alabama and Mississippi (U.S. Fish and Wildlife Service, 1987). Gopher tortoises are afforded different levels of legal protection throughout their range, but a permit is always required to possess, study, directly take, harass, or relocate gopher tortoises.

One of the most important aspects of gopher tortoise ecology is the burrow. Burrow characteristics are dependent on the characteristics of the habitat, but length typically ranges between 3-6 m, depth averages 2 m, and the angle approximates 45°. The burrow is a refuge from inclement weather, fire, and predators, but is also a focal point of activity within the habitat. Hundreds of species of invertebrates and vertebrates have been documented using and/or occupying gopher tortoise burrows (Jackson and Milstrey, 1989; Lips, 1991). Because the burrow is such an integral component of many upland habitats, the gopher tortoise has been called a keystone species (Eisenberg, 1983). Its requirement for access to high, dry habitats in which to dig burrows frequently leads to conflicts with human development and expansion. Extirpation of gopher tortoises and their burrows from an area could presumably lead to the disappearance or decline of associated commensal species (Franz, 1986a, b; Kent and Snell, 1994).

Each tortoise digs several burrows (McRae et al., 1981; Smith et al., 1997) which it uses extensively for thermoregulation (Anderson, 2001). When environmental conditions (e.g., temperature) are unfavorable, a tortoise may not emerge from a burrow for several months (McRae et al., 1981). A widely used method to establish presence and/or estimate the size of the tortoise population on a site is counting burrows. Typically, burrow openings are visually categorized, based on external characteristics, as “active”, “inactive”, or “abandoned” (table 1), according to criteria originally established by Auffenberg and Franz (1982) and revised by Cox et al. (1987). Tortoise population sizes are estimated by summing the number of active and inactive burrows (abandoned burrows are exempted from further consideration after the initial classification procedure) and multiplying that sum by a burrows-to-tortoises correction factor. The correction factor is an estimate of the expected proportion of burrows actually occupied by a tortoise. The credibility of using a correction factor that is not site-specific is suspect, but that problem is not addressed in this paper. Resulting population estimates are used for demographic studies and, in cases where the habitat will be destroyed for development, to determine permit requirements (i.e., mitigation rates for “take” permits when no attempt will be made to save tortoises or burrows from the development activity, and relocation site requirements when the tortoises will be removed from harm’s way to either on-site or off-site reserves). Therefore, accurate classification of burrows based on external characteristics and the resulting tortoise population estimates are critical.

Another method for estimating tortoise population size is by directly surveying the interior of burrows using a camera (Buskirk and Fiedler, 1986; Kent et al., 1997). A typical burrow camera system is comprised of three main parts: 1) a camera head within a PVC body; 2) a flexible PVC tube (2 cm diameter conduit) that houses the power and video cables connecting the camera head to the display unit; and 3) a small video monitor. High intensity infrared LEDs are mounted on the front of the camera head, allowing use of the camera in complete darkness without disturbing animals in the burrow. The flexible PVC tube with the camera head on the end is pushed/twisted down into the burrow while the monitor is watched. In recent years, these cameras have become portable and relatively inexpensive. Currently, the Florida Fish and Wildlife Conservation Commission (FFWCC) does not accept the camera method for surveying burrows to estimate population sizes for permitting purposes, but burrow cameras are frequently used in a variety of other circumstances (e.g., research, education outreach).

We suspected that burrow classification (and, therefore, the determination of burrow occupancy rates) based on external characteristics was inaccurate and highly subjective. On Cape Canaveral Air Force Station in east-central Florida, gopher tortoises were to be relocated from three abandoned launch complexes scheduled for cleanup of polychlorinated biphenyl (PCB). This project presented an opportunity to test the following questions: 1) how subjective is the classification of burrows based on external characteristics?; 2) is the classification of burrows based on external characteristics influenced by observer experience and/or site familiarity?; and 3) is the burrow camera a reliable means of determining if a burrow is, or is not, occupied by a gopher tortoise? Because every burrow at the site would be excavated after our surveys were completed, we viewed the excavation results as the “truth” of occupancy that could be compared to survey results.

Methods

Cape Canaveral Air Force Station (CCAFS) is a 6,394 ha installation located on the Atlantic coast in Brevard County, east-central Florida. Cape Canaveral lies on a relatively young barrier island that began forming approximately 7,000 years ago (Brooks, 1972). Soils near the coast are alkaline with many shell fragments, generally of the Palm Beach or Canaveral sands types, and the dominant habitat types where this study occurred are coastal dune and coastal strand (Schmalzer et al., 2001).

Launch Complexes (LC) 14, 15, and 16 were built in 1957-1958 and have supported several different space and defense programs. LC 14 and 15 were deactivated in 1967, and LC 16 was deactivated in 1988 (U.S. Army Construction Engineering Research Laboratories, 1993; New South Associates, 1996). Some of the habitat has since reverted back to native dune and strand vegetation, while portions are maintained on an infrequent basis as ruderal mowed grass. Because of the overall disturbed nature of the sites, and the close proximity to some of the best natural tortoise habitat in the vicinity (R. Seigel pers. comm., Smith pers. obs.), these abandoned launch complexes (and others) support large populations of gopher tortoises.

We assembled a team of five biologists with extensive gopher tortoise field experience (3, 9, 12, 15, and 19 years). Three of us had experience in the local area, while the other two had done most of their work in north Florida and South Carolina. The habitat at the launch complexes that would be impacted was thoroughly searched for burrows in late February 2000. The timing of the PCB cleanup project necessitated that our study be conducted in late February; however, this did not pose a problem as gopher tortoises in central Florida are active all year long whenever daily temperatures are suitable (Smith et al., 1997). The high temperatures during the week preceding our study were 24°C-25.5°C (Drese, 2000), sufficiently warm for gopher tortoises to be active. Each burrow was marked with a stake and numbered individually. During a one day time period, each biologist independently inspected every burrow and classified it based on external characteristics as “active”, “inactive”, or “abandoned”. Criteria for classification followed those described by Cox et al. (1987; table 1), which are currently used by the FFWCC for habitat development permitting purposes. Care was taken not to disturb the sandy mounds in front of burrows, and the classifications were not discussed among the biologists while the surveys were being done.

The following day, four of the five biologists formed two teams of two people each and surveyed all burrows (active, inactive, and abandoned) using burrow cameras (manufactured by Southern Ecosystems Research, Auburn, AL). Burrows were classified as “occupied” by a tortoise, “unoccupied” by a tortoise, or, in cases where burrow configuration made surveying difficult, “undetermined”. Both teams surveyed each burrow within a few minutes of each other, and as soon as the second team was finished, the burrow entrance was blocked so that nothing could subsequently enter or exit the burrow. Camera surveys were completed in 1.5 days. Burrow excavations with a backhoe began in the afternoon of the second day and excavations were completed within one week.

External characteristics classification results were assessed separately for each team member and then compared to the rest of the team. The importance of both prior tortoise experience and familiarity with local conditions were tested using the odds ratio (Rosner, 1995). Significance level was set at 0.05. Burrow camera survey results were compared between the two teams and to the excavation results.

Results

Ninety-five burrows were marked and classified using external characteristics. For nine burrows (9%), all five of the team members agreed that the burrow was either

Table 2. Results from gopher tortoise burrow external characteristics classifications ($n = 95$ burrows), Cape Canaveral Air Force Station, February 2000.

Agreement/disagreement among team members	No. of burrows	% of burrows
All five team members agreed	9	9
Four agreed/one disagreed	45	47
Three agreed/two disagreed, but agreed with each other	27	28
Three agreed/two disagreed, but also disagreed with each other	11	12
Two agreed/two disagreed but agreed with each other/fifth disagreed with everyone	3	3

active, inactive, or abandoned (table 2). Forty-seven percent (45 burrows) of the time, four of us agreed, with one person disagreeing as to a burrow classification. Three people agreed and the other two disagreed (but agreed with each other) for 27 burrows (28%). In 11 cases (12%), three people agreed, and the other two disagreed with them and with each other. Finally, 3% (three burrows) of the time, two people agreed, two others disagreed with them but agreed with each other, and the fifth person disagreed with everyone else.

In cases where four people agreed and one disagreed on the burrow classification, prior experience working with gopher tortoises was important. In 29 of the 45 times this situation occurred, the person disagreeing was the one with the least experience (three years). This was significant ($0.01 < p < 0.02$). The person with the most experience (19 years) accounted for 12 of the remaining 16 disagreements, but this effect was not statistically significant.

Three of the team members had prior experience working with tortoises on CCAFS. In order to determine if familiarity with the local area affected the external characteristics classification, we analyzed the situation where three team members agreed and the other two team members disagreed but agreed with each other (27 burrows). Only eight times (30%) were the three that agreed those team members that had prior experience working with tortoises on CCAFS. This difference was not statistically significant.

Fifty-seven of the original 95 burrows were surveyed with burrow cameras (the remaining 38 burrows were determined to be outside the impact area, eliminating the need to excavate the burrows or relocate the tortoises). In 48 cases, both teams agreed that a particular burrow was either unoccupied by a tortoise ($n = 38$), occupied by a tortoise ($n = 8$), or that the occupancy could not be reliably determined ($n = 2$) (table 3). In nine cases, the two teams disagreed: one team thought a particular burrow was unoccupied while the other team called it undetermined ($n = 6$), one team said unoccupied when the other team said occupied ($n = 2$), and one team said a burrow was occupied while the other team said undetermined ($n = 1$) (table 3).

All 57 burrows that were surveyed with burrow cameras were excavated with a backhoe. The excavation results were considered to be “truth”, or the final determination of burrow occupancy by a tortoise. Forty-six burrows were empty

Table 3. Results from gopher tortoise burrow camera surveys ($n = 57$ burrows) performed by two teams, and burrow excavation results, Cape Canaveral Air Force Station, February 2000. "Agreement" resulted when the two teams concurred as to whether the burrow was occupied or unoccupied by a tortoise, or that the status could not be determined. "Disagreement" resulted when the two teams did not concur. Excavation totals were 46 unoccupied and 11 occupied.

Results	Occupancy determined using burrow cameras	Occupancy determined by excavation
48 agreements	38 unoccupied	Unoccupied
	8 occupied	Occupied
	2 undetermined	Unoccupied
9 disagreements	6 undetermined vs unoccupied	Unoccupied
	2 unoccupied vs occupied	Occupied
	1 undetermined vs occupied	Occupied

(table 3). These included the 38 burrows that were classified as "unoccupied" by both teams in the camera survey, the two burrows that were classified as "undetermined" by both teams in the camera survey, and the six burrows that were classified as "unoccupied" by one team and "undetermined" by the other. Eleven burrows were occupied by tortoises (table 3). These included the eight burrows that both teams agreed were occupied in the camera survey, the two burrows that one team called "occupied" and the other team called "unoccupied", and the one burrow that one team said was occupied, but that the other team called "undetermined".

Discussion

Our study showed that the visual classification of gopher tortoise burrows based on external characteristics was highly subjective. There was poor agreement among the five team members for 43% of the burrows surveyed. Prior experience was a significant factor influencing survey accuracy. Our least experienced team member often classified burrows differently from the rest of the team, but her three years of experience were much more than what is typical for people currently doing tortoise surveys for developments. At this time, there is no set of minimum qualifications required of surveyors prior to conducting assessments. In training classes offered by the non-profit Gopher Tortoise Conservation Initiative, 95% of the students surveyed ($n = 838$ professional biologists working with tortoises) had no formal training in gopher tortoise natural history or field techniques (Ashton and Ashton, in press). Also, 95% of the students had been "trained" by coworkers that had learned on their own in the field, and very few (8%) had read any scientific literature on gopher tortoises. Students or new employees tasked with classifying burrows should not be expected to obtain accurate, or even meaningful, survey results. This is particularly problematic when results are being used to determine development mitigation rates and relocation site requirements. Freilich and LaRue (1998) concluded that experience was not an important factor in finding desert tortoises, their burrows, or signs of tortoises. However, their study is not directly comparable to ours because it focused on detection (as opposed to burrow classification), was conducted under artificial conditions, and their definition of "experienced" was variable, sometimes including people that had participated in only one previous survey. Lack of familiarity with the landscape was not significant in our study, but that obstacle may have been outweighed by the skill of the team members. Less knowledgeable workers may be negatively affected by unfamiliar surroundings and conditions.

One of the causes of inconsistency between surveyors when using external characteristics classification is the imprecise nature of the burrow class descriptions (table 1). Distinguishing between an inactive burrow that is "occluded by debris" versus an abandoned burrow that is "covered with sticks, weeds, and grass" is strictly an interpretation made by the observer. An experienced gopher tortoise biologist will know to look at the overall shape of the burrow and condition of the apron, as well as consider any mitigating factors, such as time of year and recent rain events, before making a determination. No one on our team called any burrow "abandoned" that was actually occupied by a tortoise. However, novice surveyors may rely on one characteristic, such as vegetation or presence of tracks, to decide the classification. Considering that any burrow classified as "abandoned" is subsequently deleted from further investigation, calling inactive burrows abandoned can reduce mitigation rates and/or potentially lead to tortoise mortalities. In two separate studies, 5% and 12% of burrows that were classified as abandoned based on external characteristics were actually occupied by tortoises (Witz et al., 1991; Tuberville and Dorcas 2001). So-called "abandoned" burrows may harbor a significant portion of a population. In addition, burrows that have, in reality, been abandoned by gopher tortoises are often used by commensals (Witz et al., 1991), including federally protected species such as eastern indigo snakes (*Drymarchon couperi*) (Witz et al., 1991). The practice of ignoring so-called abandoned burrows should be reconsidered.

The burrow camera was an excellent survey tool, but there has been resistance by regulatory agencies to incorporate its use into the accepted official survey methods. As with any tool, burrow cameras are not foolproof; they must be used carefully and with common sense. The burrows we surveyed at CCAFS were near the beach in Palm Beach sand and were generally straight without side chambers. However, in other habitats and soil types, obstructions such as roots or rocks can cause a tortoise to dig a very convoluted burrow. Long-term weather conditions may also influence burrow configuration. During a relocation project on CCAFS in 1998, many burrows were excavated that were unusually deep ($>$ 8 meters) and, after the initial sloping entrance, went straight down in a corkscrew fashion (R. Smith, pers. obs.). We believe this was because of the extreme heat and drought conditions prevalent that summer which caused the tortoises to dig until they reached the cool hardpan layer under the sand. Burrows such as these are impossible to survey with a burrow camera. Nonetheless, when used under the right conditions by experienced personnel, and in conjunction with other survey techniques, burrow cameras are an invaluable resource.

Of the 57 burrows surveyed with burrow cameras by the two teams, no burrows were called occupied when they were actually empty (table 3). Twice, occupied burrows were called unoccupied by one of the teams, for an error rate of 0.02. In most survey situations, this error would be considered acceptable; however, those two errors could have ultimately been fatal for the tortoises inside the burrows. When dealing with a protected, high-profile species like the gopher tortoise, this can easily become an undesirable situation, not only for biological reasons, but also for public relations.

Three steps could be taken that would greatly improve the dependability of the currently accepted survey system. First, the classification criteria distinguishing active vs. inactive vs. abandoned burrows should be made precise and clear. Any burrow classified as abandoned should be so dilapidated that it would take considerable work by a tortoise to reopen the burrow. The distinction between active and inactive burrows could be dropped in many cases (i.e., take or relocation permit acquisitions), so that there were only two categories: potentially occupied and abandoned.

The second step is to allow and encourage the proper use of burrow cameras for surveying purposes. The burrow camera is an effective tool that can aid in the determination of burrow occupancy and lead to more reliable population estimates. In order to do the best camera surveys possible, we suggest that two experienced people examine each burrow, that the surveyors take a sufficient amount of time with each burrow, and that they do not hesitate to err on the conservative side. It is better to treat an empty burrow as though it is occupied than the opposite.

Our third suggested improvement is to require that only qualified, experienced tortoise biologists perform surveys. Untrained individuals need to accompany experienced people into the field several times or participate in other training exercises before attempting to do surveys alone.

The current gopher tortoise burrow survey methods are widely used and accepted, even though little effort has been made to validate their accuracy. As the threats to gopher tortoise populations (e.g., habitat loss, habitat fragmentation, disease, predation) persist and/or increase, reliable survey information will become even more fundamental to our goal of long-term population viability.

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References

Anderson, N.J. (2001): The thermal biology of the gopher tortoise (*Gopherus polyphemus*) and the importance of microhabitat selection. MS thesis, Southeastern Louisiana University.

Ashton, R.E., Ashton, P.S. (In press): The Natural History and Management of the Gopher Tortoise, *Gopherus polyphemus*. Kreiger Publishing Co., Melbourne, Florida.

Auffenberg, W., Franz, R. (1982): The status and distribution of the gopher tortoise (*Gopherus polyphemus*). In: North American Tortoises: Conservation and Ecology, p. 95-126. Bury, R.B., Ed., U.S. Fish and Wildlife Service, Wildlife Research Report #12.

Brooks, H.K. (1972): Geology of Cape Canaveral. In: Space-age Geology, p. 35-44. Garner, T.E., Ed., Southeastern Geology Society, Tallahassee, Florida.

Buskirk, S.W., Fiedler, D.L. (1986): A low-cost television system for exploring burrows and dens. Wildl. Soc. Bull. **14**: 185-188.

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. Florida Game and Fresh Water Fish Commission Nongame Wildlife Program Technical Report #4.

Diemer, J.E. (1992): Gopher tortoise. In: Rare and Endangered Biota of Florida, vol. III, Amphibians and Reptiles, p. 23-27. Moler, P.E., Ed., University Press of Florida, Gainesville, Florida.

Drese, J.H. (2000): Air quality summary and monitoring status at John F. Kennedy Space Center for the first quarter (January-March) 2000. Report prepared for NASA Biomedical Operations and Research Office by the Dynamac Corporation. Contract #NAS10-12180.

Eisenberg, J.F. (1983): The gopher tortoise as a keystone species. In: The Gopher Tortoise: A Keystone Species. Proceedings of the 4th Annual Meeting of the Gopher Tortoise Council, 47 pp. Bryant, R.J., Franz, R., Eds, Florida State Museum, Gainesville, Florida.

Franz, R. (1986a): The Florida gopher frog and the Florida pine snake as burrow associates of the gopher tortoise in northern Florida. In: The Gopher Tortoise and Its Community. Proceedings of the 5th Annual Meeting of the Gopher Tortoise Council, p. 16-20. Jackson, D.R., Bryant, R.J., Eds, Florida State Museum, Gainesville.

Franz, R. (1986b): *Gopherus polyphemus* (Gopher tortoise) burrow commensals. Herp. Rev. **17**: 64-65.

Freilich, J.E., LaRue, E.L. (1998): Importance of observer experience in finding desert tortoises. J. Wildl. Manage. **62**: 590-596.

Jackson, D.R., Milstrey, E.G. (1989): The fauna of gopher tortoise burrows. In: Gopher Tortoise Relocation Symposium Proceedings, p. 86-98. Diemer, J.E., Jackson, D.R., Landers, J.L., Layne, J.N., Wood, D.A., Eds, State of Florida Game and Fresh Water Fish Commission, Nongame Wildlife Program Technical Report #5.

Kent, D.M., Snell, E. (1994): Vertebrates associated with gopher tortoise burrows in Orange County, Florida. Fla. Field Nat. **22**: 8-10.

Kent, D.M., Langston, M.A., Hanf, D.W., Wallace, P.M. (1997): Utility of a camera system for investigating gopher tortoise burrows. Fla. Sci. **60**: 193-196.

Lips, K.R. (1991): Vertebrates associated with tortoise (*Gopherus polyphemus*) burrows in four habitats in south-central Florida. J. Herpetol. **25**: 477-481.

McRae, W.A., Landers, J.L., Garner, J.A. (1981): Movement patterns and home range of the gopher tortoise. Amer. Midl. Nat. **106**: 165-179.

New South Associates. (1996): 45th Space Wing Cultural Resource Management Plan for Patrick Air Force Base and Cape Canaveral Air Force Station, Brevard County, Florida. New South Associates, Stone Mountain, Georgia.

Rosner, B.A. (1995): Fundamentals of Biostatistics, 4th Ed. Wadsworth Publishing Co., Belmont, CA.

Schmalzer, P.A., Hensley, M.A., Dunlevy, C.A. (2001): Background characteristics of soils of Kennedy Space Center, Merritt Island, Florida: Selected elements and physical properties. Fla. Sci. **64**: 161-190.

Smith, R.B., Breininger, D.R., Larson, V.L. (1997): Home range characteristics of radio tagged gopher tortoises on Kennedy Space Center, Florida. Chelonian Conser. Biol. **2**: 358-362.

Tuberville, T.D., Dorcas, M.E. (2001): Winter survey of a gopher tortoise population in South Carolina. Chelonian Conser. Biol. **4**: 182-186.

U.S. Army Construction Engineering Research Laboratories. (1993): Determination of Eligibility of Launch Complexes and Related Facilities for Listing on the National Register of Historic Places at Cape Canaveral Air Force Station, Florida. Tri-Services Cultural Resources Research Center, Champaign, Illinois.

U.S. Fish and Wildlife Service. (1987): Determination of Threatened Status for Gopher Tortoise (*Gopherus polyphemus*). 52 FR 25376-25380.

Witz, B.W., Wilson, D.S., Palmer, M.D. (1991): Distribution of *Gopherus polyphemus* and its vertebrate symbionts in three burrow categories. Amer. Midl. Nat. **126**: 152-158.

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