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Article *in* Chelonian Conservation and Biology · December 2016

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Source: Chelonian Conservation and Biology, 15(2):231-237.
Published By: Chelonian Research Foundation
DOI: http://dx.doi.org/10.2744/CCB-1181.1
URL: http://www.bioone.org/doi/full/10.2744/CCB-1181.1

Chelonian Conservation and Biology, 2016, 15(2): 231–237

Aggression, Combat, and Apparent Burrow Competition in Hatchling and Juvenile Gopher Tortoises (*Gopherus polyphemus*)

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ABSTRACT. – Adult North American tortoises (*Gopherus* spp.) engage in aggressive interactions with conspecifics when competing for mates and burrows. However, aggressive interactions have not been widely reported in hatchling and juvenile tortoises. We describe aggressive interactions between wild hatchling and juvenile gopher tortoises (*Gopherus polyphemus*) based on video recordings collected at tortoise burrows. Immature tortoises usually inhabited burrows alone but occasionally shared them. Presence of multiple individuals inside burrows hindered tortoise movements in burrows. Hatchlings or juveniles exhibited overt aggression toward similar aged/sized conspecifics in at least 6 of 13 (46%) encounters, and cameras may have failed to detect aggression occurring inside burrows. Hatchlings and juveniles also exhibited aggressive responses to foreign objects that were similar in appearance to small tortoises. Aggressive behaviors resembled those of adults and included repeated ramming, pushing, biting, and flipping. Young tortoises may respond aggressively to conspecifics at burrows because the presence of additional individuals constrains thermoregulatory and antipredator movements within these important microhabitats. Social interactions appear to play a greater role in the ecology of hatchling and juvenile gopher tortoises than previously recognized.

KEY WORDS. – behavior; reptile; social interactions; time-lapse video; turtle

Aggression can enhance an individual's ability to compete for resources or mates and features prominently in the ecology of many turtle species, including North American tortoises (*Gopherus* spp). For example, adult male desert (*Gopherus agassizii*) and gopher (*Gopherus polyphemus*) tortoises engage in combat (i.e., repeated ramming, flipping) with other males, presumably because it increases access to reproductive females (Auffenberg 1977; Niblick et al. 1994). In another context, female desert tortoises and, sometimes, gopher tortoises defend nests against potential predators (Barrett and Humphrey 1986; Zylstra et al. 2005; Gienger and Tracy 2008; Grosse et al. 2012; Agha et al. 2013; Dziadzio and Smith 2015). Adult gopher tortoises also aggressively compete with conspecifics for burrows (Douglas 1976; McRae et al. 1981; Diemer 1992), a key resource that requires lengthy investments of time to construct and is used extensively for thermoregulation, predator avoidance, and other important activities (e.g., sleeping, mating, and nesting; Douglass and Layne 1978; Landers et al. 1980; Johnson et al. 2007).

Although aggression is a common characteristic of North American tortoises in the genus *Gopherus*, most observations of aggression in this group, and turtles in general, involve mature individuals. Immature tortoises do not compete for mates or defend nests and are generally considered docile. Immature gopher tortoises do, however, occasionally cohabitate burrows (McRae et al. 1981; Diemer 1992; Butler et al. 1996; Pike and Antworth 2005), and this proximity provides a setting where agonistic interactions might be predicted if, similar to adult tortoises, immature tortoises also compete for burrows. Diemer (1992) reports an instance of burrow competition between two "subadult" (large, nearly mature) gopher tortoises. Adult-like behaviors might be expected in animals approaching maturity, but an observation by Butler and colleagues (1996) suggests that hatchlings also aggressively defend burrows. The authors report "a hatchling ramming another who had encroached on the defender's burrow apron," but did not share additional information about the encounter. Aside from this account we are unaware of other reports of aggression in hatchling or small juvenile gopher tortoises.

It is unclear whether aggression is common in young gopher tortoises because few studies have focused on interactions among immature individuals of this species. Young gopher tortoises are difficult to observe, in part because they tend to retreat into burrows quickly when approached (Wilson et al. 1994; T.A.R., *pers. obs.*). In a detailed study of juvenile gopher tortoise ecology, Wilson et al. (1994) reported on the activity budgets and movements of young tortoises fitted with radio transmitters but did not include information regarding social behaviors. Pike and Antworth (2005) presented several observations

of burrow cohabitation without overt aggression but also identified the need for future investigation focusing on potential social interactions in hatchling and juvenile gopher tortoises.

We used time-lapse video cameras to study the behavior of young gopher tortoises at a site in southwest Georgia. Our observations included several instances of aggressive interactions with behaviors such as ramming and flipping that are well known for adult gopher tortoises. Here, we describe these aggressive interactions and discuss their potential functions in the ecology of hatchling and juvenile gopher tortoises.

METHODS

We conducted this study on Arcadia Plantation (30°45′N, 84°0′W), located in Thomas County in southwest Georgia. The study site was dominated by mature (> 80 yrs) longleaf pine (*Pinus palustris*) forest and included the Wade Tract, an 80-ha research area that has never been heavily cut and contains many old trees (> 250 yrs; Platt et al. 1988). Ground cover on both Arcadia Plantation and the Wade Tract was dominated by wiregrass (*Aristida stricta*), oaks (*Quercus* spp.), and a diverse assemblage of other native plants (Ambrose 2001). Soils at the site are a complex mosaic of sand and clay (US Department of Agriculture, Natural Resources Conservation Service 2016). The study area was managed using frequent prescribed fire (≤ 2-yr return intervals).

During June to September 2011, December 2011 to January 2012, March to September 2012, December 2012, April to October 2013, and September to October 2014, we studied hatchling and juvenile gopher tortoise thermoregulatory and antipredator behavior at the site. Observations of tortoise interactions were incidental to these studies and were made using time-lapse cameras (primarily Plotwatcher Pro, Day 6 Outdoors, Inc., Columbus, GA) that recorded tortoise activity at hatchling (age, 0–1 yr) and juvenile burrows continuously (usually one frame per second) during daylight hours. For some of this research (e.g., thermoregulatory movements), we avoided recording at burrows known to contain multiple tortoises, and for other research, we specifically filmed burrows known to contain multiple tortoises to observe interactions. Because of this nonrandom collection of video data, we did not estimate burrow sharing frequency. All observations of tortoise interactions were of wild animals. Interactions involving individuals reared in the laboratory and subsequently released as yearlings back into the site (in September 2014) were not included in this study.

We scored a tortoise as aggressive if it rammed or repeatedly pushed another individual (Weaver 1970; Auffenberg 1977; Ruby and Niblick 1994). We also documented other agonistic behaviors such as biting, flipping, and withdrawal (Weaver 1970; Auffenberg 1977; Ruby and Niblick 1994). When possible, we identified unique individuals by size, location within the study site, or presence of radio transmitters or miniature iButton temperature loggers (Maxim Integrated Products, Sunnyvale, CA) affixed to shells (used to study thermoregulatory and antipredator behavior at the site). Three hatchlings (3L10R, 3R10R, 10R) and two juveniles (2R3L, 330.630) documented to engage in overt aggression had radio transmitters and/or iButtons attached to their carapaces at the time of observations.

RESULTS

Tortoise Encounter Summary and Aggression. — Video cameras documented hatchling or juvenile tortoises cohabitating (sharing a burrow overnight) in 5 burrows. Cameras also documented hatchlings or juveniles briefly visiting 8 burrows already occupied by an immature conspecific without sharing the burrow overnight. These encounters, observed at 12 different burrows (one burrow was both a cohabitation and brief visitation site), usually involved a pair of tortoises, but in 2 instances, 3 immature tortoises cohabitated a burrow (Supplemental Video File 1; available at http://dx.doi.org/10.2744/CCB-1181.1.s.1). Cameras documented tortoises cohabitating up to 8 consecutive days, but tortoises may have cohabitated longer because cameras did not record the beginning and end of each cohabitation event.

The presence of a second or third tortoise in a burrow hindered free movement of occupants in and out of burrows in each of five observed instances of burrow cohabitation (Supplemental Video File 1). Qualitatively, burrow dimensions (widths and heights) were similar to those of resident tortoises, making it difficult or impossible for individuals to pass one another in the burrow shaft.

We observed aggression in 6 of 13 (46%) instances of cohabitation or brief visits to occupied burrows. In total, cameras recorded 4–6 (some tortoises were unmarked) individual hatchlings and 5 individual juveniles exhibiting overt aggression toward another immature tortoise. In 3 brief visits (< 8 min) where aggression was not observed, the visiting tortoises only looked inside the occupied burrow entrance or briefly entered before leaving. These tortoises may have left in response to the presence of the resident tortoise. However, some tortoises cohabitated burrows for many days, without engaging in overt aggression.

Hatchling–Hatchling Aggressive Interaction 1. — The most dramatic instance of aggression involved 2 hatchlings (age, ∼9–10 mo), and included repeated pushing, apparent biting, and flipping (Fig. 1). A video of this interaction is available in the online version of this manuscript (Supplemental Video File 2; available at http://dx.doi.org/10.2744/CCB-1181.1.s.2). At 1118 hrs on 2 June 2013, the resident hatchling (ID: 3L10R, carapace length = ∼61 mm, mass = ∼57 g) left its burrow apron, presumably to forage. At 1145 hrs, a visiting hatchling (ID: 3R10R, carapace length = ∼61

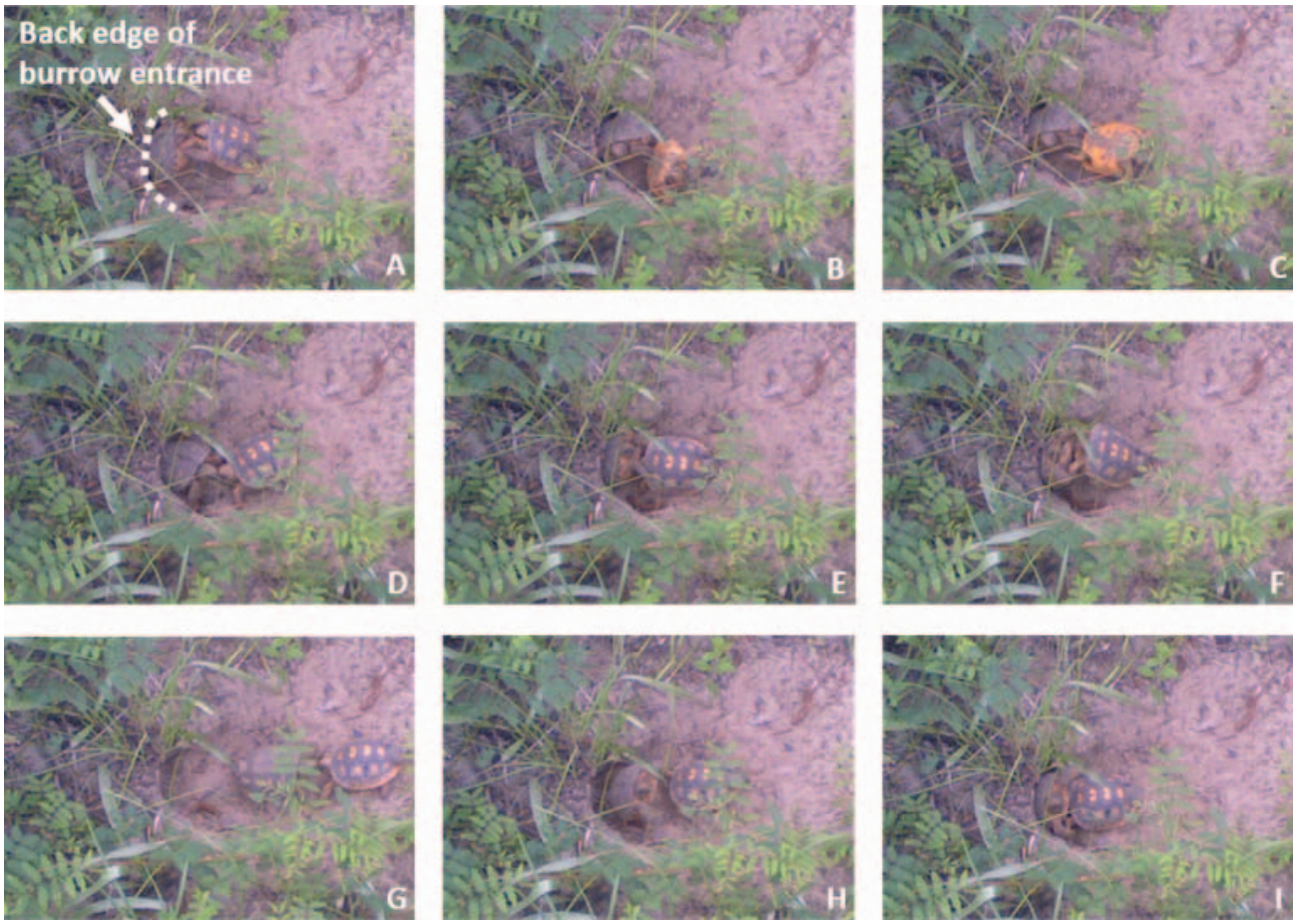

Figure 1. Combat between a resident (right in all frames) and visiting (left) hatchling (age = ~9–10 mo) gopher tortoise on 2 June 2013 at Arcadia Plantation in southwest Georgia. (A–C) The visiting tortoise flipped the resident onto its carapace; (D–F) upon righting itself, the resident pushed the visitor into a vertical orientation against the back of the burrow entrance; (H–J) following additional interactions (described in the text), the resident again pushed the visitor into a vertical orientation against the burrow entrance. Shortly thereafter (not shown) the visiting tortoise left and returned to its burrow, suggesting that aggressive interactions may limit burrow sharing by hatchling tortoises. (Color version is available online. A video of this interaction is available at http://dx.doi.org/10.2744/CCB-1181.1.s.2.)

mm, mass = ~66 g), whose burrow was located ~4 m away, arrived at the resident's burrow and entered. At 1148 hrs, the resident hatchling returned and immediately entered its burrow, which still contained the visitor. At 1223 hrs, the resident hatchling reemerged, and 2 min later the visitor appeared in the burrow entrance behind the resident, repeatedly extending its head toward the resident, possibly biting at an iButton temperature logger attached to the resident's rear vertebral scute. At 1226 hrs, the resident turned around and faced the burrow entrance and the visitor (who was still in the entrance). Both hatchlings immediately began to push against each other with their forelimbs and gular protrusions, keeping their heads withdrawn during the exchange (Fig. 1A). The opposing forces of the tortoises' (bodies) caused their anterior plastrons to rise off the ground (Fig. 1A). This continued for several seconds until the visitor (still in the burrow entrance) flipped the resident onto its carapace (Fig. 1B–C).

After being overturned, the resident hatchling required 50 sec to right itself and landed partially atop the visitor. Both remained motionless for an additional 40 sec. Next, the resident turned toward the visitor (which faced outward from the burrow), withdrew its head, and used its gular protrusion, forelimbs, and carapace to ram the visitor against the entrance until it was pinned against the entrance in a nearly vertical orientation (Fig. 1D–F). Both tortoises then resumed pushing and biting each other with their heads retracted until the visitor retreated into the burrow. The resident remained at the surface facing the burrow.

About 3 min later, the visitor reemerged and advanced toward the resident until the resident moved backward one body length. Following this movement, the resident charged the visitor, once again pushing it backward into a vertical orientation against the burrow entrance. The resident repeatedly rammed the visitor until the visitor pushed past the resident and returned to its own burrow nearby (observed by another camera located at the visitor's burrow). The resident continued to bask in front of the burrow for several more minutes before entering inside.

Hatchling–Hatchling Aggressive Interaction 2. — Around midday on 26 June 2012, one of us (T.A.R.) briefly placed a metal tablespoon inside a hatchling burrow. Shortly after holding the spoon in the entrance, an unmarked hatchling started to repeatedly ram the spoon and continued to do so as the spoon was pulled slowly out of the burrow. The hatchling was captured as it followed the spoon out of the burrow, and a second hatchling (unidentified) emerged from the burrow within seconds, apparently in response to the exit of the first individual. T.A.R. was unable to capture the second tortoise before it reentered the burrow.

Shortly before 0900 hrs on the following day, we returned the hatchling (still unmarked) to its burrow (which still contained the other unidentified hatchling) and set a camera to monitor interactions. The camera first observed several hatchling movements in and out of the burrow without overt aggression. Aggression was apparent starting at 1131 hrs, when one hatchling attempted to reenter the burrow, but was unable to do so because the other tortoise occupied the entrance. Although it was difficult to interpret from the video, it appeared that as the outermost hatchling attempted to reenter the burrow, the hatchling in the entrance pushed back several times and prevented it from entering. After a few minutes, the hatchling in the entrance went deeper into the burrow and the outermost hatchling entered the inside edge of the burrow. The outermost hatchling reemerged to bask again at 1138 hrs. At 1148 hrs, the outermost hatchling again turned to face the entrance as if attempting to enter, but the other hatchling blocked the entrance and appeared to push the outermost hatchling backward as it attempted to enter. After unsuccessfully attempting to reenter the occupied burrow, the outermost hatchling left the area at 1152 hrs.

Hatchling–Hatchling Aggressive Interaction 3. — At 1040 hrs on 3 August 2012, an unmarked hatchling tortoise approached a burrow while the marked resident hatchling (ID: 10R) was inside. The visiting hatchling attempted to enter the burrow, at which point the resident hatchling (now in the burrow entrance) repeatedly pushed back against the visitor. This sequence repeated itself several times. Because the resident hatchling was in the entrance during the entire encounter, it was not possible to observe additional details. At 1048 hrs, the visiting hatchling left the area. Hatchling–hatchling aggressive interactions 2 and 3 occurred several meters apart and, therefore, could have involved the same individuals (the one marked hatchling [10R], was marked after interaction 2 occurred).

Hatchling–Juvenile Aggressive Interaction 1. — At 1134 hrs on 7 August 2013, a juvenile tortoise (ID: 2R3L, age = 2 yrs, carapace length = ~83 mm) was inside its burrow when a hatchling tortoise (age, ~11 mo) visited and entered just inside the burrow. About 25 sec after entering the burrow, the hatchling turned around and faced out of the burrow entrance. Less than a minute later, the hatchling emerged fully with the larger juvenile repeatedly pushing it from behind. The juvenile had its head withdrawn into its shell as it pushed the hatchling, suggesting that it was responding aggressively toward the visitor. Once on the burrow apron, the hatchling turned around to face the juvenile before leaving the area soon thereafter at 1136 hrs.

Juvenile–Juvenile Aggressive Interactions 1 and 2. — At 1034 hrs on 29 July 2012, a juvenile tortoise (ID: 330.630, age = ~9 yrs, carapace length = 143 mm) that was basking in front of its burrow rapidly entered inside. A few seconds later, another slightly larger juvenile (unmarked) arrived at the burrow, stopped just before the entrance, and faced inside. At 1039 hrs, the visitor advanced toward the burrow, and the resident juvenile emerged to the entrance and repeatedly rammed the intruder, which retreated backward about three-quarters of a body length. The two tortoises sat motionlessly facing each other for about 2 min. Then, the resident aggressively advanced toward the visitor, which responded by backing up to the edge of the burrow apron, where the aggressive interaction continued under some vegetation and mostly out of camera view. At 1043 hrs, the resident quickly backed into its burrow while the visitor remained at the edge of the burrow apron. From 1043 to 1045 hrs, the visitor advanced incrementally toward the burrow entrance until it partially entered the burrow at 1053 hrs. The resident was still inside the burrow. Then at 1058 hrs, both tortoises started repeatedly ramming each other head-on with their heads withdrawn into their shells. At 1105 hrs, the larger visiting tortoise left the area.

We observed a second aggressive interaction involving 2 different unmarked juvenile tortoises (~6-yr-olds, age estimated from video). The two tortoises were inside a burrow when the camera started recording at 0708 hrs on 3 September 2014. Also present inside the burrow was a third tortoise, a yearling that was raised in the laboratory and later released back into the site on 1 September 2014. Only the yearling tortoise emerged from the burrow on 3 September. On the following morning, the yearling left the burrow area without returning, and the two larger juveniles emerged shortly thereafter. They moved between the burrow and surface several times without overt aggression but shortly before 1500 repeatedly pushed each another back and forth in the burrow entrance before entering inside for the remainder of the day.

Additional Aggressive Interactions Between Tortoises and Objects. — We observed 2 additional tortoises (1 hatchling and 1 juvenile) respond aggressively toward objects placed inside or near burrows. Around midday on 7 June 2013, one of us (T.A.R.) attempted to remove an iButton miniature temperature logger from 10 cm within hatchling 3R10Rs (visitor from Interaction 1) burrow using a pair of long-nosed pliers. Hatchling 3R10R advanced toward the pliers. Later, T.A.R. wiggled a (~1.5 cm in diameter) dowel rod in the burrow to simulate the bobbing head of a visiting tortoise. The hatchling

repeatedly rammed the dowel as if it was confronting an intruder. The hatchling responded in the same manner to multiple insertions of the dowel into its burrow. Although it advanced toward the burrow entrance as T.A.R. slowly removed the dowel, it did not fully emerge.

On 28 July, 30 July, and 4 August 2013, a camera documented a 3-yr-old juvenile (3R3L) repeatedly ramming/pushing, with its head partially withdrawn, an operative temperature model that had been placed earlier on the burrow apron. The grey model was of similar size, shape, and color of a tortoise but did not have a head or limbs. We did not document any other tortoises clearly interacting with models. In all of the above examples, the vigor of the tortoises' interactions with the objects (spoon, dowel rod, or temperature model) indicated aggressive behavior.

DISCUSSION

Although infrequent and difficult to observe, aggression likely plays an important role in the ecology of hatchling and juvenile gopher tortoises by influencing access to burrows. Young tortoises come into contact with one another at burrows where they either respond aggressively or cohabitate for prolonged periods without overt aggression (Butler et al. 1996). Varied responses to conspecifics may reflect individual or situational differences but may also be an artifact of the fact that cameras did not document activities inside burrows where tortoises spent most of their time. Therefore, some individuals may have engaged in unobserved agonistic interactions in burrows. Notably, the observed aggressive behaviors were remarkably similar to those of adult *Gopherus* and included repeated ramming, pushing, and flipping (Auffenberg 1977; Niblick et al. 1994; Ruby and Niblick 1994). Hatchlings also sometimes bit each other during these exchanges.

Hatchling and juvenile tortoises may respond aggressively to conspecifics because the presence of a second individual inside a burrow interferes with thermoregulatory and antipredator movements. Tortoise burrows are not much wider than the resident tortoise, making it difficult or impossible for individuals to pass one another in the burrow shaft, which even in the case of juvenile tortoises, can be several meters long. Young gopher tortoises at our site basked extensively just in front of their burrows and made frequent movements in and out of burrows, presumably to regulate body temperature (T.A.R., *pers. obs*.). The presence of a conspecific hindered such movements. Hatchlings and juveniles cannot remain at the surface in open habitats for extended periods during hot weather (operative temperatures at our site frequently exceed 50°C, T.A.R., *pers. obs*.), and aggressive interactions at burrows can affect the ability of a hot individual to escape into an occupied burrow before overheating.

Burrow cohabitation may hinder antipredator movements in young tortoises. Hatchling and small juvenile gopher tortoises have soft shells and are vulnerable to many predators, including snakes, mammals, and birds (Fitzpatrick and Woolfenden 1978; Butler and Sowell 1996; Epperson and Heise 2003; Stevenson et al. 2010; Stevenson 2014). In our study population, basking tortoises (hatchlings, juveniles, and adults alike) usually retreat rapidly into burrows when approached (T.A.R., *pers. obs*.). However, we routinely observed instances in which the presence of a tortoise just inside a burrow prevented another individual from entering deeper inside. Often the outermost tortoise was seen at the burrow entrance frantically pushing on the tortoise that was deeper in the burrow in an effort to enter further inside. Sharing burrows may place individuals that are slower to enter burrows at greater predation risk than individuals occupying burrows alone.

Young tortoises do not always respond aggressively to conspecifics that visit their burrows, perhaps because aggressive behaviors involve energy expenditure and carry some risk. As we document, hatchlings may flip one another during combat, and it is conceivable that in certain situations a young tortoise may be unable to right itself before overheating. For example, the flipped tortoise in our observation (Interaction 1) required nearly 50 sec to right itself, which is similar to the righting time required by other hatchlings we have observed overturned in the field. However, hatchlings may not be able to right themselves in loose sand if there is no vegetation or structure nearby to provide the grip required for the righting maneuver (T.A.R., *pers. obs*.). Additionally, aggression that involves biting may result in injuries. We observed this firsthand when we placed 2 hatchlings together in a container in the laboratory as part of other work. In that case, one individual bit the other, producing a scratch just next to the eye. Finally, our observations of hatchlings repeatedly ramming both dowel rods and metal spoons placed inside burrows and advancing to burrow entrances or even fully emerging in response to foreign objects, suggest that similar misplaced aggression toward a predator could result in increased predation risk.

The accounts presented here, along with that of Butler et al. (1996), indicate that hatchling and juvenile gopher tortoises exhibit a wider range of social behaviors than previously recognized. Aggressive behaviors of immature tortoises are similar to those of adult conspecifics, and probably play a role in determining burrow use patterns, particularly as young tortoises come into contact with conspecifics at burrows. We conclude that, although ecologically important, such interactions are probably underreported, perhaps in large part because of the wary nature of immature gopher tortoises and their tendency to quickly hide in burrows when approached. However, time-lapse cameras provided windows into the activities and behaviors of young tortoises, including their social interactions. Future studies could examine potential costs

associated with burrow cohabitation (e.g., constraints on thermoregulation and predator avoidance), individual variation in aggressive tendency, factors that may underlie such potential variation (e.g., personality, relatedness, age, sex), and how aggressive interactions influence patterns of burrow use and cohabitation in young gopher tortoises.

ACKNOWLEDGMENTS

We thank Jaclyn Smolinsky and Brent Mills for valuable assistance in the field. Maryann Fitzpatrick and Wolfgang Nadler graciously helped to construct radio transmitters used in this study and 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 awarded to T.A.R. 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. David Delaney and the US Army Construction Engineering Research Laboratory generously loaned additional equipment used in this research. 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. We are very appreciative of housing support provided by Tall Timbers Research Station at different times throughout the project. Nick Blase and the Eco Sem group at Drexel provided comments on an earlier version of this manuscript. This work was conducted in accordance with the Drexel University Institutional Animal Care and Use Committee (protocol 19661) and the Georgia Department of Natural Resources (permit: 24821).

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Received: 14 August 2015

Revised and Accepted: 22 September 2016

Handling Editor: Jeffrey E. Lovich