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Movement and Survival to Winter Dormancy of Fall-Released Hatchling and Head-Started Yearling Gopher Tortoises

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Abstract.—Gopher Tortoise (*Gopherus polyphemus*) populations are declining throughout the southeastern United States. Range-wide conservation efforts include identifying populations that do not currently meet viability criteria but are suitable candidates for population enhancement. We investigated the potential role of head starting as a recovery tool by releasing hatchling and head-started yearling Gopher Tortoises as pairs ($n = 28$) into adult burrows in fall and comparing their movements and survival until winter dormancy. Head-started yearlings experienced higher predicted survival than did hatchlings (87.7% vs. 56.5%). Head-started individuals also tended to move greater distances between burrows and established dormancy burrows further from their release burrows, but the differences were not significant. Most individuals of both groups used a small number of closely spaced burrows, although hatchlings took longer than head-started individuals to establish their first burrow (11.3 vs. 4.4 d on average) and a higher proportion were depredated or censored before establishing a burrow (35.7% vs. 10.7%). The paired release design provides strong experimental evidence that head-started yearling Gopher Tortoises experience at least a short-term survival advantage over hatchlings, while exhibiting comparable fidelity to the release site. Soft-release pens were not necessary to promote high site fidelity in our study, but the decision as to whether or not to use them at other release sites may be dictated by the predator community and what is practical to implement. We contend that head starting shows promise as a recovery tool for Gopher Tortoises and that hard releases may be a worthwhile option for managers to consider.

Gopher Tortoise (*Gopherus polyphemus*) populations are declining throughout the southeastern United States (Auffenberg and Franz, 1982; Diemer, 1986; Smith et al., 2006), primarily as a result of habitat loss and degradation, but also due to subsidized predators, invasive species, disease, and collection and harvest by humans (Smith et al., 2006; U.S. Fish and Wildlife Service [USFWS], 2011). In 1987, the Gopher Tortoise was federally listed as threatened in the western portion of its Coastal Plain distribution – western Alabama, Mississippi, and southeastern Louisiana (USFWS, 1987). However, populations of Gopher Tortoise in the eastern portion of the range have now declined sufficiently to warrant federal protection, although listing is currently precluded (USFWS, 2011). Populations have declined even on protected lands where the Gopher Tortoise was once presumed secure (McCoy et al., 2006).

Recent conservation measures for Gopher Tortoises have focused on evaluating long-term viability of extant populations (Smith et al., 2006). Based on three independent research efforts (McCoy and Mushinsky, 2007; Tuberville et al., 2009; Styrsky et al., 2010) and consensus among species experts, the Gopher Tortoise Council (2013) identified the following criteria as critical thresholds for maintaining minimally viable Gopher Tortoise populations: at least 250 adults at a density of $\geq$0.4 tortoises/ha, evidence of recruitment, and occurrence on a minimum reserve size of 100 ha of suitable, actively managed habitat. Applying the Gopher Tortoise Council criteria to survey results from standardized line-transect distance sampling (Smith et al., 2009; Castellón et al., 2015; Stober et al., 2017) has led to improved knowledge regarding the current status of extant populations (Gopher Tortoise Council, 2014). One of the high-priority actions specified in the Range-Wide Conservation Strategy for the Gopher Tortoise (USFWS, 2013) is to identify populations that do not currently meet viability criteria but that are suitable candidates for population enhancement or restocking (USFWS, 2013; Gopher Tortoise Council, 2014).

Although wild-to-wild translocations have been successfully used to establish or augment Gopher Tortoise populations (Ashton and Burke, 2007; Tuberville et al., 2008), such efforts rely on the availability of tortoises displaced from sites elsewhere. Head starting, or the process of rearing juvenile turtles in captivity through their most vulnerable period (Burke, 2015; Spencer et al., 2017), is one potential technique that could be used to boost depleted populations. Head starting allows hatchlings to reach larger body size classes more quickly compared to their counterparts living under natural conditions, presumably making them less susceptible to predation (Heppell et al., 1996; O'Brien et al., 2005). Furthermore, hatchlings obtained from field-collected nests offer a more predictable source of animals and, when collected from robust populations, minimize effects on donor populations (Heppell, 1998; Quinn et al., 2016). The head-starting technique has historically garnered considerable controversy (Frazer, 1992; Seigel and Dodd, 2000; Burke, 2015), but there is increasing recognition of its potential role, particularly when used in concert with other management actions (Turtle Conservation Fund, 2002; Spencer et al., 2017).

Gopher Tortoises are among the most commonly translocated herpetofauna (Seigel and Dodd, 2000), yet head starting has only recently been explored as a management tool for the species. Tuberville et al. (2015) reported on postrelease monitoring of head-started yearling Gopher Tortoises opportunistically released at two protected sites in Georgia and South Carolina. Several years of mark–recapture revealed that head-started Gopher Tortoises have the potential to experience postrelease annual survival as high as 80%. A subsequent study by Quinn et al. (2018) used radiotelemetry to estimate survival and reported that 8–9 mo head-started Gopher Tortoises exhibited 70% annual survival when predation risk during soft-release penning was mitigated. However, annual tortoise survivorship can vary among release groups and across even small spatial scales because of variation in predation risk (Tuberville et al., 2005; Quinn et al., 2018), which may confound

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FIG. 1. Hatchling gopher tortoise (left) and yearling head-started gopher tortoise (right) released as a pair at the entrance of an unoccupied adult tortoise burrow.

perceived benefits of head starting without a direct comparison to hatchlings. To account for spatial and temporal variability in survivorship and more explicitly quantify the benefits of head starting, we released hatchling and head-started yearling Gopher Tortoises as pairs directly into adult burrows and compared their postrelease movement and survival until winter dormancy.

MATERIALS AND METHODS

Study Site.—The recipient site for hatchling and head-started yearling Gopher Tortoises was the Yuchi Wildlife Management Area (YWMA) in Burke County, Georgia (33.11°N, 81.74°W). YWMA is a 3,127-ha protected area managed by Georgia Department of Natural Resources (GADNR) and is located near the northeastern edge of the Gopher Tortoise's range, lying immediately south of the Georgia Fall Line on the Upper Coastal Plain. Prior to state ownership, silviculture practices destroyed much of the suitable Gopher Tortoise habitat at the YWMA resulting in a depleted tortoise population. Despite extensive replanting with Longleaf Pine (*Pinus palustris*) yielding 1,894 ha (61%) of potentially suitable Gopher Tortoise habitat, Smith et al. (2009) found that the Gopher Tortoise population remained depleted. The YWMA was thus considered a suitable site for population augmentation. The release sites on YWMA for tortoises in this study were the same as in Bauder et al. (2014) and Quinn et al. (2018), which were centrally located within the managed area and had suitable habitat consisting of a sparse canopy primarily of Longleaf Pine, an absent midstory, and a diverse understory. See Quinn et al. (2018) for a more detailed description of YWMA.

Experimental Design.—In fall 2015, we released 10 recently hatched neonates, hereafter referred to as hatchlings, and 10 yearling tortoises that had been head started indoors for 1 yr (hereafter head starts). In fall 2016, we released 18 hatchlings and 18 head-started individuals, for a combined total of 28 hatchlings and 28 head-started individuals between the two releases. We obtained all individuals by collecting eggs from wild Gopher Tortoise populations in Georgia: St. Catherines Island in Liberty County, Reed Bingham State Park in Cook County, and YWMA. Quinn et al. (2016) provides a description of egg collection methods, incubation, and hatching success. We briefly held hatchlings in captivity for an average of 26.3 d (range: 6–47 d) prior to release so that all animals released in a year could be released in groups. We reared head-started individuals on St. Catherines Island and at the University of Georgia's Savannah River Ecology Laboratory (Aiken County, South Carolina) for an average of 386 d (range: 349–409 d) prior to release, as described in Quinn (2016). Prior to the release of tortoises, we determined body mass to the nearest 0.1 g using a DeltaRange® Mettler PE 3,600-g scale (Mettler Toledo) and straight midline carapace length (SCL; from nuchal to pygal) to the nearest 0.1 mm using dial calipers (Mitutoyo). We report body mass and SCL means (± 1 SE). We permanently marked tortoises by notching a unique combination of marginal scutes (Ernst et al., 1974). We attached radiotransmitters to the fourth vertebral scute of head-started individuals (Advanced Telemetry Systems Model R1680, 3.6 g) and hatchlings (Advanced Telemetry Systems Model R1655, 1.2 g) using WaterWeld epoxy (J-B Weld®) or Loctite® 5 min Epoxy (Henkel Corporation), respectively.

We conducted hard releases (i.e., no initial penning) in fall 2015 and fall 2016 by placing a paired hatchling and head-started yearling just outside the entrance, and facing into, an intact adult tortoise burrow (Fig. 1). We released 56 tortoises: 10 head-start/hatchling pairs on 14 September 2015, 10 pairs on 26 September 2016, and 8 pairs on 04 October 2016. We did not release head-start/hatchling pairs into the same burrow as another pair during the same release year. We radiotracked tortoises at least once each week following their release until winter dormancy (15 November of release year) so that we could document movement and survival. We selected 15 November as the threshold for overwintering based on other Georgia studies (McRae et al., 1981; Harris et al., 2015; Quinn et al., 2018).

Analysis.—We combined data from 2015 and 2016 releases for a sample size of 28 head-start/hatchling pairs as survival did not differ between years for either hatchlings ($\chi^2_{df=1} = 0.03$, $P = 0.86$) or head starts ($\chi^2_{df=1} = 0.14$, $P = 0.71$). Pooling data also increased the likelihood of detecting any significant differences between treatment groups in our analyses. We documented survivorship to dormancy based on whether they were dead, alive, or censored (i.e., lost from the study because of transmitter detection failure or inability to locate when scoping burrows) as of 15 November in the year they were released. We estimated survival using the Kaplan-Meier estimator for staggered entry and used log-rank tests to compare survival curves between head starts and hatchlings (Pollock et al., 1989) in the *asbio* package in Program R (Aho, 2015; http://CRAN.R-project.org/package=asbio). Survival data are presented as mean ± 95% confidence intervals.

We based all movement analyses on burrow locations used by radiotracked tortoises. We used the spherical law of cosines (Movable Type Ltd., 2015) to calculate step distances (i.e., linear distances between successive burrow locations) and linear displacement from release sites (i.e., linear distance from the tortoise's release burrow to each subsequent burrow). For each tortoise, we calculated average displacement (i.e., average linear distance from the release burrow to other burrows used) and final displacement from release burrow (i.e., linear distance from release burrow to burrow occupied at beginning of dormancy on 15 November), and summarized values across individuals. Because tortoise mortality resulted in different monitoring durations among individuals, we only report movement data for individuals that survived until 15 Novem-

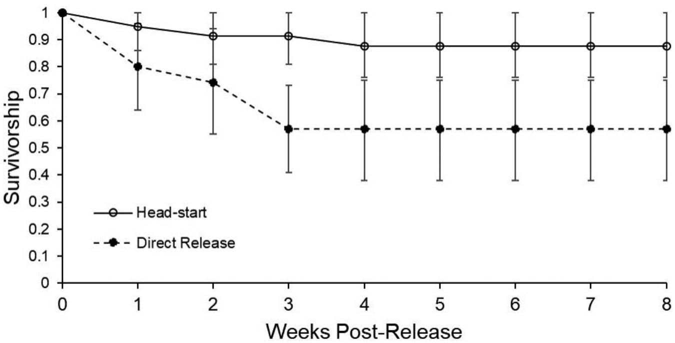

FIG. 2. Survivorship until winter dormancy (15 November, Week 8) for directly released hatchlings ($n = 28$) and head-started yearling ($n = 28$) gopher tortoises released in fall at Yuchi Wildlife Management Area in Burke County, Georgia. Survival curves represent weekly Kaplan-Meier survivorship with staggered entry.

ber of their release year. We compared movements of head starts and hatchlings using a two-tailed Student's *t*-test.

RESULTS

At release, head-started individuals averaged 133.0 ± 6.1 g (range 75.9–192.5 g) and 84.6 ± 1.6 mm SCL (range 68.9–192.5 mm), and hatchlings averaged 32.6 ± 0.7 g (range 24.4–39.2 g) and 49.1 ± 0.4 mm SCL (44.0–52.9 mm). Of the original 28 head-started individuals that we released, 24 (85.7%) survived until winter dormancy, 3 (10.7%) died, and 1 was censored. Of the 28 hatchlings, 16 (57.1%) survived until dormancy, 10 (35.7%) died, and two were censored. In each case of censored tortoises in our study, the transmitter signal was emitted from inside the original release burrows and the signal never moved to another location. Even when using a burrow scope, we could not detect the tortoise and survival status of censored tortoises remained unknown (i.e., left censored). Kaplan-Meier survivorship estimates revealed that head starts experienced significantly higher survivorship to dormancy (87.7%, confidence interval [CI]: 75.4–100%) than did hatchlings (56.5%, CI: 38.3–74.9%; $\chi^2_{df = 1} = 5.81$, $P = 0.02$; Fig. 2). Of the three deceased head-started individuals, two were depredated by mammals and one dispersed beyond the managed property and into a roadway with steep embankments. We intervened with the wayward individual and returned it to the managed property and although this tortoise ultimately survived to dormancy, we considered it a translocation failure as it dispersed beyond the study area and likely would have died if not for our intervention. Of the 10 hatchlings that died, 6 were depredated by fire ants (*Solenopsis invicta*), 2 by Eastern Coachwhips (*Coluber flagellum*), and one by an unknown mammal based on teeth marks.

Of the 28 hatchlings, 10 (35.7%) never established a burrow before being depredated or censored from the study. The remaining 18 hatchlings established their own burrow on average within 11.3 d of release (range 1–31 d). Six had dug their own burrow within 2 d and 10 had dug their first burrows within 7 d. One hatchling that survived the study period never established a burrow, only using a shallow pallet as refuge. Of the 28 head-started individuals, only 3 (10.7%) failed to establish a burrow before being depredated or censored. The remaining 25 established a burrow within an average of 4.4 d of release (range 1–21 d). Of the 24 head-started individuals that survived until winter dormancy, 15 had dug their first burrow within 2 d of release, and 22 had dug their first burrow within 7 d. Although all hatchlings that survived to dormancy constructed only a single burrow, five (20.8%) head-started individuals that survived to dormancy constructed at least two burrows, and one constructed three.

We monitored the 16 hatchlings and 24 head-started individuals that survived until winter dormancy for an average of 52 d (range: 42–62 d). Head-started tortoises tended to move more than did hatchlings in terms of average distance moved between successive burrows, average distance between release burrows and other burrows used by an individual tortoise, and distance between dormancy burrow and release burrow. None of the comparisons, however, were statistically significant (all $P > 0.05$; Table 1). Overall, movements by both release groups were limited, but varied among individuals. At the termination of the study, 21 of the 24 (87.5%) surviving head-started tortoises were within 50 m of their release burrow (mean = 14.6 m), with the others having established dormancy burrows 147 m, 158 m, and 277 m from their release burrow. Excluding the individual that never created a burrow, 86.7% of surviving hatchlings had dormancy burrows within 15 m of their release burrow (mean = 6.0 m), with the other two at 29.3 m and 30.2 m.

DISCUSSION

Our study demonstrated that yearling head-started Gopher Tortoises experienced significantly higher survival to dormancy but exhibited similar movement patterns when compared to hatchlings released simultaneously. Of the 28 head-start/hatchling pairs hard released into adult Gopher Tortoise burrows, survival to dormancy was 30% higher in head-started individuals when compared to hatchlings (87.7% vs. 56.5%, respectively). Although we only monitored tortoises for a short period following release (≤8 wk), previous studies have shown that most mortality of hatchling or head-start Gopher Tortoises occurs within the first 30–60 d of release or emergence from the nest (Epperson and Heise, 2003; Pike and Seigel, 2006; Smith et

TABLE 1. Mean movement comparisons between head-start and hatchling Gopher Tortoises that survived from their fall release until winter dormancy (15 November) at Yuchi Wildlife Management Area in Burke County, Georgia. Mean step length is the average distance moved by an individual tortoise between successive burrows. Mean displacement is the linear distance between release burrow and each of the other burrows used by an individual. Final displacement is the distance between dormancy burrow and release burrow. Data are presented as means ± 1 SE (ranges). *P* values represent Student's *t*-test (two-tailed) comparisons; n = number of tortoises (of the 28 of each group release) that survived until first dormancy and are included in movement analyses.

Parameters	Head start ($n = 24$)	Hatchling ($n = 16$)	*t* value	df	*P* value
Mean step length (m)	31.0 ± 10.8 (0.9–267.3)	8.3 ± 2.9 (0.9–30.2)	0.91	45	0.11
Mean displacement (m)	41.5 ± 13.5 (0.0–276.7)	9.2 ± 1.9 (0.9–30.2)	0.94	45	0.07
Final displacement (m)	37.0 ± 13.0 (2.4–276.7)	8.7 ± 2.2 (0.9–30.2)	0.92	38	0.09

al., 2013; Dziadzio et al., 2016; Quinn et al., 2018; Radzio et al., 2019; but see Butler and Sowell, 1996).

Few survival estimates are available for head-started Gopher Tortoises. The most comparable estimates are from Radzio et al. (2019), who reported 63.3–76.7% survival to dormancy for head starts released as yearlings in southwest Georgia. A previous study at YWMA reported survival of 8–9-mo-old head starts from release in spring to first winter dormancy (4–5 mo of monitoring) at 72.7% for the first release group ($n = 11$), but only 43.3% for a group released the following year ($n = 30$; Quinn et al., 2018). Only two studies report survivorship data for wild yearling Gopher Tortoises. Butler and Sowell (1996) radiotracked 14 hatchlings in northern Florida and found that of the 10 that survived to yearlings, all were depredated before the end of their second year. Similar results were observed in Mississippi by Epperson and Heise (2003). Wilson (1991) radiotracked 1–4-yr-old wild juveniles and estimated bimonthly survival during October–November (similar to our monitoring period) at 69.0%.

Several studies have investigated hatchling survival, with annual survival ranging from 0 to 53% among releases (Butler and Sowell, 1996; Smith, 1997; Epperson and Heise, 2003; Pike and Seigel, 2006; Perez-Heydrich et al., 2012; Tuberville et al., 2015, 2020), unless predators were excluded or removed (Smith et al., 2013; Dziadzio et al., 2016). Few studies specifically report survival to first winter dormancy, but Epperson and Heise (2003) found that only 13 of 48 (27.1%) released hatchlings survived to winter dormancy. Collectively, these studies confirm the tenet that mortality of hatchling and even yearling Gopher Tortoises is high and variable among sites and among years (Pike and Seigel, 2006), making it difficult to compare results from different studies. Thus, incorporating an experimental component is crucial for interpreting results (Tuberville et al., 2015; Quinn et al., 2018). Our study is the first to monitor survival of hatchling and head-started yearling Gopher Tortoises concurrently at the same study site and provides compelling evidence that head-started yearlings experience higher survival than hatchlings during the first 2 mo following release, when they are most vulnerable to predation.

The survival advantage of head-started individuals over hatchlings is presumably driven largely by the increased size of head-started tortoises. Released head starts were larger than released hatchlings in this study (69–93 vs. 45–53 mm MCL) and wild-caught yearlings in other studies (48–82 mm MCL depending on the site; Mushinsky et al., 1994; Aresco and Guyer, 1999; Harris, 2014). Postrelease survival has been found to increase with increasing size at release in both head-started Mojave Desert Tortoises (*Gopherus agassizii*) and Northern Red-bellied Cooters (*Pseudemys rubriventris*) (Haskell et al., 1996; McGovern et al., 2020). Age, which is often correlated with size, has also been found to influence survival in juveniles of other turtle species, including Hermann's Tortoises (*Testudo hermanni*) and European Pond Turtles (*Emys orbicularis*; Fernández-Chacón et al., 2011; Arsovski et al., 2018). However, we cannot rule out the possibility of behavioral differences that could influence survival of head-started yearlings and directly released hatchlings.

Of the metrics that we quantified, the two experimental groups varied most obviously in their burrowing behavior. Although head starts and hatchlings used similar numbers of burrows between release and dormancy, head starts were quicker to dig their first burrow than were hatchlings (average of 4.4 d vs. 11.3 d, respectively). Within 2 d of release, 60% of head starts had constructed a burrow compared to only a third of hatchlings. Within 7 d of release, 88% of head starts but only 55% of hatchlings had constructed their first burrow. The greater latency by hatchlings to establish a burrow likely explains their lower survival, as evidenced by the higher proportion of individuals that died or that were censored from the study before having established a burrow (35.7% vs. only 10.7% in head-started yearlings). Two separate studies on released juvenile Desert Tortoises found that surface activity was an important predictor of survival, with animals located outside a burrow more frequently being less likely to survive their first year following release (Daly et al., 2019; McGovern et al., 2020).

No other study exists that compares burrow use of hatchling and yearling Gopher Tortoises at the same study site. However, Radzio et al. (2019) reported burrowing behavior by head-started yearling Gopher Tortoises in southwest Georgia that is similar to what we observed in our study, with 47% of released yearlings initiating a burrow within 2 d of release and 76.7% within 7 d of release. In contrast, fewer hatchlings in our study dug burrows within the first 7 d as compared to the 76.9% reported for Gopher Tortoises by Butler et al. (1995) in Florida. In our study, the average time that elapsed between release and first burrow construction by Gopher Tortoise hatchlings was four times that observed for hatchlings in Mississippi (2.9 d; Epperson and Heise, 2003). We speculate that the abundance of fire ants at our study site may have contributed to the extended time hatchlings took to dig their first burrow when compared to both head starts at our site and hatchlings in other studies. The percent of hatchling mortalities that was attributed to fire ants in our study was twice that reported by Epperson and Heise (2003) and 1.5 times that of head-started individual Gopher Tortoises previously reported at our study site (Quinn et al., 2018). In addition to increased mortality upon exposure to fire ants, hatchling Gopher Tortoises may move farther and use more locations when ambient fire ant density is high compared to when it is low (Dziadzio et al., 2016). Rather than occurring in distinct mounds, fire ants at our site appear to be diffusely distributed throughout the soil (Quinn et al., 2018). Burrow depth is positively correlated with tortoise size in juvenile Gopher Tortoises (Holbrook et al., 2015), with the larger head-started yearlings more likely to dig beyond the 10-cm depth where fire ants forage (Markin et al., 1975; Gravish et al., 2012) but where hatchling burrows are likely largely restricted to (Dziadzio et al. 2016). Thus, hatchlings are vulnerable to fire ants both inside and outside of their burrows and tend to change burrow locations more often when fire ants are more abundant (Dziadzio et al., 2016). Hatchlings may also be more reluctant to establish a burrow in areas with relatively high fire ant abundance such as at our site. The timing of our study coincided with the time of year when surface foraging activity by fire ants can start to taper off (Porter and Tschinkel, 1987, Vogt et al., 2003) but when fire ant use of refuges is greatest and can negatively affect refuge use by vertebrates (Stahlschmidt et al., 2018).

We observed that both directly released hatchling and head-started yearling Gopher Tortoises exhibited remarkably high site fidelity, with only one individual (a yearling) leaving the boundaries of YWMA. On average, tortoises from both treatment groups used only a few ($\leq$3) closely spaced burrows near their original release burrow, although individuals within a treatment group, particularly head-started turtles, varied in their movement behavior (Table 1). Head-started individuals appeared to move greater distances than did hatchlings both between successive burrows (31.0 m vs. 8.3 m) and between dormancy burrows and release burrows (37.0 m vs. 8.7 m) although apparent differences were not statistically significant. Our results mirrored those reported in the literature for released hatchlings and head-started Gopher Tortoises, as well as for wild juveniles. In two separate studies from Florida, hatchling Gopher Tortoises moved an average of 8.0 m between successive burrows during their first year (Pike, 2006) and 17.1 m in the first 2 yr following release (Butler et al., 1995). Similarly, wild juveniles typically use a few burrows that are on average ≤16.0 m apart (McRae et al., 1981; Diemer, 1992; Wilson et al., 1994). Juvenile Gopher Tortoises that were head started for 8–9 mo and released at YWMA in prior years moved on average 11.8–23.5 m between successive burrows, depending on the release group (Quinn et al., 2018). Hatchlings in Mississippi settled into dormancy burrows that were an average of 35 m from the nest site from which they hatched (Epperson and Heise, 2003). Butler et al. (1995) did not report distance between release burrow and first dormancy burrow but did state that the hatchlings that survived to become yearlings were found in burrows located an average of 81.4 m from the release burrow at the beginning of their second winter dormancy. In southwest Georgia, burrows used by head-started yearlings in the first month following release were within 29.4 m of their release location, and those that survived until 2 yr of age were still using burrows within an average of 29.9 m of their original release location (Radzio et al., 2019). The maximum distance traveled by an individual in our study from its original release was by a head-started yearling that traveled 277 m away compared to 119 m and 170 m by head-started Gopher Tortoises in other studies (Quinn et al., 2018; Radzio et al., 2019; respectively).

Based on the movement patterns exhibited by tortoises in our study, we do not believe that soft-release pens are necessary to encourage high site fidelity in directly released hatchlings or in head-started yearling Gopher Tortoises. In fact, the use of small soft-release pens during a previous release at YWMA made confined tortoises vulnerable to fire ant predation (Quinn et al., 2018). Depending on the distribution and size of soft-release pens or the density of animals inside them, soft-release pens can also concentrate tortoises and their burrows into a small area where high tortoise density could attract raccoons or other mesopredators (Holbrook et al., 2015; Quinn et al., 2018). However, there may be complex trade-offs in terms of predation risk by fire ants versus vertebrate mesopredators (Dziadzio et al., 2016). At least in some cases, survivorship of juvenile Gopher Tortoises can be enhanced when they are placed in soft-release pens or pens that are designed to exclude vertebrate predators (Smith, 1997; Smith et al., 2013; Dziadzio et al., 2016). So, although soft-release pens may not be required to promote site fidelity (Radzio et al., 2019), pens may confer a survival benefit and thus merit further consideration (Diemer, 1986; Tuberville et al., 2015). The decision as to whether or not to use soft-release pens in association with releases of juvenile Gopher Tortoises may largely be influenced by the predator community at the release site and that which is logistically feasible to implement.

Regardless, our study provides strong experimental evidence that head-started yearling Gopher Tortoises experience at least a short-term survival advantage over hatchlings, while exhibiting comparable fidelity to the release site. We contend that head starting shows promise as a tool for augmenting depleted populations of Gopher Tortoises and further, that hard releases may be a worthwhile option for managers to consider. Although we were not able to monitor animals beyond dormancy initiation, longer-term monitoring would provide information critical for further evaluating the effects of head starting on survival and lend credence to its utility as a recovery tool. Likewise, similar studies conducted at other sites across the species' range would provide insight into how widely applicable our results are. Finally, we recommend that future efforts investigate the optimal duration of head starting and whether longer head-starting periods confer an additional survival advantage.

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