HEAD-STARTING AS A MANAGEMENT COMPONENT FOR GOPHER TORTOISES (GOPHERUS POLYPHEMUS)

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Abstract.—Viability models of turtle populations have shown that after adult survivorship, juvenile survivorship is the most influential parameter affecting population persistence. This suggests that increasing juvenile survivorship, such as through head-starting, might be a useful management strategy. Little is known about survivorship and ecology of juveniles of most turtle species, including even wellstudied species such as the Gopher Tortoise (Gopherus polyphemus). Limited data on the fate of headstarted tortoises further constrains attempts to evaluate head-starting as a management tool. We summarize our experiences head-starting Gopher Tortoise hatchlings as part of reintroduction efforts at Savannah River Site (SRS), South Carolina, USA, and St. Catherines Island (SCI), Georgia, USA, and compare survivorship of head-started hatchlings with juveniles manipulated using other techniques. Hatchlings exhibited nearly 100% survivorship during the captive head-start period, but survivorship during the first year post-release varied among cohorts: 17 of 32 (53.1%) 2001 SRS hatchlings, seven of seven (100%) 2005 SCI hatchlings, and one of 32 (3.1%) 2006 SCI hatchlings. For two cohorts, head-started hatchlings performed as well as older non-head-started juvenile tortoises. At least 20.0% of St. Catherines Island neonates that we released into temporary predator-proof cages shortly after hatching (i.e., without head-starting) were known to have survived through their first winter dormancy. Survivorship for all manipulated hatchlings (regardless of treatment) was lowest during the first year post-release. The potential role of head-starting as a management tool merits further investigation. We recommend that future studies include an experimental component to allow critical evaluation of the techniques implemented.

Key Words.—direct-release; *Gopherus polyphemus*; Gopher Tortoise; hatchling; head-start; juvenile; survivorship; translocation

INTRODUCTION

Of the approximately 317 species of turtles and tortoise recognized worldwide, 42% are considered to be threatened with extinction and many of the remaining species have yet to be evaluated (Buhlmann et al. 2009; International Union for the Conservation of Nature. 2009. IUCN Red List of Threatened Species. Available from http://www.iucnredlist.org [Accessed 8 January 2011]). As chelonians become increasingly

threatened, management interventions typically regarded as a last resort, such as translocation, captive breeding, and head-starting (Seigel and Dodd 2000), are becoming increasingly accepted as instrumental conservation components (Turtle Conservation Fund 2002). Head-starting turtles, the process by which hatchlings are reared in captivity until they reach a size at which they are less vulnerable to predation (Frazer 1992), is unlikely to compensate for reduced adult survivorship resulting from human-related disturbances (Heppell et al. 1996; Heppell and Crowder 1998). shortly after hatching) on SCI. However, head-starting could potentially be used to augment an existing population or reestablish an extirpated population if threats to adult survivorship have been mitigated (McDougal 2000), provided that head-started individuals are as robust as wild-recruited individuals (Heppell et al. 1996).

Although the Gopher Tortoise (Gopherus *polyphemus*) is probably the most frequently translocated chelonian species (Seigel and Dodd 2000) and has been the subject of numerous translocation experiments (e.g., Heise and Epperson 2005; Tuberville et al. 2005, 2008; Ashton and Burke 2007), it has received little attention in terms of head-starting. One hindrance to evaluating the need for and the potential effectiveness of head-starting in Gopher Tortoises is the lack of data on natural recruitment and survivorship of juveniles in wild populations. Wilson (1991) is one of the few studies to provide data on mortality rates of juvenile Gopher Tortoises. Juvenile tortoises are notoriously difficult to study because of their secretive nature, limited above-ground activity, and small size-factors that limit detectibility of both the tortoises and their burrows (Wilson 1991; Morafka 1994; Wilson et al. 1994). However, intensive monitoring of populations established through the release of marked animals provides an ideal setting in which to monitor juvenile survivorship.

Here we summarize juvenile mark-recapture data from Gopher Tortoise reintroduction projects at two study sites where we have conducted head-starting: Savannah River Site, South Carolina (SRS), and St. Catherines Island, Georgia (SCI). The goals of this paper are to: (1) report release size and post-release survivorship of head-started Gopher Tortoises at each study site; (2) compare survivorship of head-started juveniles to translocated juveniles (i.e., offspring produced at a donor site and translocated to a recipient site as a juvenile) on the SRS; and (3) compare survivorship of head-started juveniles to direct-released hatchlings (i.e., offspring released

MATERIALS AND METHODS

Savannah River Site.—The study population was translocated from an industrial development site in McIntosh County, Georgia, USA (hereafter, the "donor" site), to the Savannah River Site (SRS) in Aiken County, South Carolina, USA, in August and September 2001. The SRS is an 800 km² reserve owned by the U.S. Department of Energy, and its forests and wildlife are managed by the U.S. Forest Service (White and Gaines 2000). At the time of the translocation, the SRS did not support an extant resident population of Gopher Tortoises, although they were historically common in the region (Holbrook 1842). The release site was located in the northeast corner of the SRS and was comprised primarily of 50-60 y Longleaf Pine (Pinus palustris) occurring on Lakeland and Troup series soils. The U.S. Forest Service manages the release site to maintain habitat conditions for the Red-cockaded Woodpecker (Picoides borealis) through periodic winter and early growing season burns. A more detailed study site description can be found in Tuberville et al. (2005).

We captured 74 live tortoises (39 adults and sub-adults, 35 juveniles; see Tuberville et al. 2005 for further details) at the donor site and translocated them to the SRS. During the translocation process, we also encountered seven nests at the donor site. We transported clutches to the SRS, where they were placed in incubators at 30°C until hatching. The resulting 32 hatchlings were head-started in the laboratory from Fall 2001 until their release the following active season. We housed hatchlings in small groups in large, shallow plastic tubs on a substrate of commercial rabbit pellets and exposed to 12 h of light per day using UVA-UVB fluorescent bulbs . We placed heat strips under the bins at either end to provide a thermal gradient (temperatures not recorded) and provided artificial shelters (clay pots cut along the median axis to form halves

approximately 11 cm deep \times 11 cm wide \times 6 Live Trap LLC, Tomahawk, Wisconsin, USA) cm tall placed on rabbit pellet substrate). Three times per week, we fed hatchlings a variety of fresh greens sprinkled with calcium carbonate (JurassiCalTM dry calcium powder; Seachem Laboratories, Inc., Madison, Georgia, USA) ad libitum and we soaked hatchlings in warm water for 30 min prior to each feeding. Water was also provided in shallow dishes and changed three times weekly.

We marked all tortoises by notching unique combinations of marginal scutes. We recorded shell measurements (only mid-line carapace length [CL] to nearest mm reported here) and weight (to nearest 0.1 g) of head-started tortoises at hatching, prior to release, and on each subsequent recapture. We also monitored weight weekly during the head-starting period. Likewise, we recorded shell measurements and weight of translocated juveniles prior to their release on the SRS, prior to removal of their enclosure, and on each subsequent recapture.

We released head-started hatchling tortoises 12 June 2002 into starter burrows inside a 1 ha enclosure to encourage site fidelity and facilitate monitoring. The enclosure was already occupied by 12 adult and sub-adult Gopher Tortoises translocated as part of the same study (see Tuberville et al. 2005 for further details). We constructed starter burrows using a post pounder to drive an 8 cm diameter pipe approximately 30-40 cm into the ground at a 30° angle (Fig. 1). The pipe and soil core were then removed from the ground, creating an artificial burrow. We used the soil core to create a small mound of sand (simulating a burrow apron) outside the newly constructed tunnel. We created at least two or three starter burrows for each released tortoise and strategically placed burrows to provide herbaceous cover over the burrow entrance. We removed the enclosure wall 23 September 2002.

We targeted head-started tortoises for capture during one to two week trapping sessions in Fall and Spring 2003-2006. We positioned collapsible wire live traps (Models 201, 202; Tomahawk

with trap doors at burrow entrances, secured using landscaping stakes, shaded with burlap or natural cover objects, and checked at least twice daily. We also frequently encountered headstarted tortoises and their burrows incidentally while we monitored translocated adults and subadults, which we radio-tracked at least three times per week 2002–2005.

We assigned the 35 translocated juveniles (ages one to nine, 66-180 mm CL) to three release groups such that each release group was comprised of 11-12 juveniles and had similar size distributions. In September 2001, we placed each release group in a small circular enclosure (3.5 m diameter, 92 cm tall aluminum flashing) with at least one manually-constructed starter burrow available for each tortoise (Table 1). We held tortoises in enclosures until the following spring, when we removed the enclosure walls. During their confinement, we offered supplemental food to tortoises two or three times per week when they were active. Prior to enclosure removal, we inventoried the enclosures to document survival of translocated juveniles during their first winter at the recipient site. We monitored juveniles following their release using the same techniques described for head-started tortoises.

St. Catherines Island.—Our other study population was located on St. Catherines Island (SCI), a 5,670 ha privately owned island off the coast of Liberty County, Georgia, USA. Gopher Tortoises were not native to the island but have become established through a series of releases of approximately 110-120 tortoises from multiple source populations starting in the 1980s (Tuberville et al. 2011). The release site, located at the northern end of the island, was a former cattle pasture with a sparse overstory of mature mixed pines (Pinus spp.) and an understory comprised primarily of non-native grasses. The open understory conditions were maintained through mowing. Some portions of the habitat were mowed each year



FIGURE 1. Construction of release burrows for head-started Gopher Tortoises (*Gopherus polyphemus*) on Savannah River Site, Aiken, South Carolina, USA. Burrows were created by driving a hollow pipe into soil at an angle (top left) and removing the soil core (top right). Excess soil was then used to create an apron outside burrow entrance (bottom left). Multiple starter burrows were created for each hatchling released (bottom right). (Photographed by Tracey D. Tuberville).

with each portion mowed on a three-year rotation. More information on the study site and study population can be found in Tuberville et al. (2008).

During 2006–2009 we obtained clutches of eggs from the field or by inducing gravid females to oviposit as part of a mating system study (Tuberville et al. 2011). In 2006, we artificially incubated all clutches at 28–30°C. In subsequent years, we only artificially incubated eggs we collected from gravid females; we protected field-collected nests in situ with wire mesh covers until shortly before hatching (late August), when we transferred them to artificial incubators to complete incubation. In addition, we obtained a 2005 cohort of seven hatchings from a local school group shortly after hatching (Table 1).

We head-started the 2005 and 2006 cohorts in captivity until the spring following hatching. We reared hatchlings in small groups in large, shallow plastic tubs on a substrate of rabbit pellets and provided cardboard hide boxes. We maintained animals indoors but the interior room was flanked by outdoor enclosures, exposing tortoises to natural light. Temperatures in the interior room generally ranged from 21–26°C, but heat lamps that we placed at one end of the tubs provided a thermal gradient with maximum temperature of 29–31°C. We exposed hatchlings to natural day-night light cycles, which we supplemented with UVB lights for approximately 8 h/day. We also periodically moved hatchlings outdoors for brief basking periods (several hours) when con-



FIGURE 2. Photo of release cage used for direct-release Gopher Tortoise (Gopherus polyphemus) hatchlings on St. Catherines Island, Georgia, USA. Each cage was temporarily installed and shaded with Saw Palmetto fronds near an abandoned adult burrow, and removed once hatchlings were able to expand one of the starter burrows provided or to excavate their own. (Photographed by Veronica Greco).

ditions allowed. We offered hatchlings a mixture hinged lid of galvanized small-mesh wire fencing. of fresh greens daily, which we periodically supplemented with native food plants, particularly legumes (family Fabaceae) and Narrowleaf silkgrass (Pityopsis graminofolia). We soaked animals three times per week.

We released the 2005 and 2006 head-started hatchlings into starter burrows using methods similar to those described above for the SRS. The 2007, 2008, and 2009 cohorts were not headstarted but were released shortly after hatching (hereafter, "direct-released" hatchlings). We typically released hatchlings in groups of 10-15 into protective release cages temporarily installed near an abandoned adult burrow. Release cages $(190 \text{ cm long} \times 122 \text{ cm wide} \times 33 \text{ cm high; Fig.})$ 2) consisted of a four-sided wood frame with a

We buried the bottom sides of the wood frame 5-10 cm in the ground. Inside the release cages, we constructed hatchling burrows as previously described (Fig. 1). After placing hatchlings in release cages, we secured lids with heavy-duty straps to prevent predator access and covered the lids with natural cover objects to provide shade. Release cages remained in place for two to four weeks to allow hatchlings to select and expand one of the burrows provided or to excavate their own. During this time, we checked hatchlings at least every other day and offered them a combination of salad greens and cuttings of native food plants. Although the release cages were small and resulted in high densities of hatchlings, we think the portable cages had an overall positive

TABLE 1. Summary of Gopher Tortoise (Gopherus polyphemus) hatchling and juvenile manipulations by cohort for each study site - Savannah River Site (SRS), South Carolina, USA, and St. Catherines Island (SCI), Georgia, USA. "No. individuals" are number of individuals released; "no. clutches" indicates number of clutches represented by released hatchlings. Translocated juveniles include animals from multiple cohorts (ages one to nine at time of release). Data from 2007 SCI cohort were not included in analyses due to lack of sufficient monitoring of corresponding release sites.

Cohort	No. clutches	No. individuals	Treatment	Monitoring
SRS				
2001	7	32	head-started	2002-2006
multiple	unknown	35	translocated juveniles	2002-2006
SCI				
2005	unknown	7	head-started	2006-2010
2006	8	32	head-started	2007-2010
2007	16	92	direct release + release cages	N/A
2008	7	30	direct release + release cages	2009-2010
2009	9	56	direct release + release cages	2010

effect on survivorship by protecting naïve hatch- due to spatially-variable sampling effort, we lings from predators until they began seeking cover and digging their own burrows.

We marked and measured all hatchlings using the same techniques described for SRS. In addition, while head-started tortoises were in captivity, we recorded weight weekly and shell measurements at least monthly. We were not able to record carapace length at hatching for the 2005 cohort.

We chose release sites based on qualitative evidence of successful natural recruitment and juvenile survivorship, and on our perceptions of whether sites could support additional tortoises. Our selection of specific locations for release cages was influenced by availability of a nearby abandoned adult burrow (for hatchlings to use as temporary refuge after release cages were removed) and by forage abundance (Fig. 3).

We targeted released hatchlings for trapping during one- to two-week fall (September or October) trapping sessions in 2007–2010, using the same techniques as described for the SRS. In addition, we also recaptured released hatchlings during our ongoing efforts to trap juveniles naturally recruited on the island in 2006-2010. We also incidentally encountered them while we performed other research activities. However,

present only data for those release sites subjected to targeted sampling (although we include all capture types for those sites in the analysis).

Statistical analyses.—We combined all capture records within years to construct post-release encounter histories for each individual. We considered individuals to be alive in a given year if we captured them live at least once during that year or in any subsequent year. Because detectibility of juveniles is typically low and not all individuals alive and remaining in the study area will be encountered in any given year, our reported survivorship estimates are minimum estimates and may underestimate true survivorship. We used two-way ANOVA without replication to test for the main effects of year and juvenile treatment (i.e., head-started or translocated) on annual juvenile survivorship at SRS. We tested for differences in release size (CL and mass) between the 2005 and 2006 SCI head-started cohorts using a t-test. Because the duration of head-starting varied among the head-start groups, we used individual t-tests to test for differences in daily size increase (CL and mass) between the SRS and SCI head-start groups, and between the 2005 and 2006 SCI cohorts. We performed all statistical



FIGURE 3. Map of St. Catherines Island, Georgia, USA, showing release locations for head-started and direct-released Gopher Tortoise (*Gopherus polyphemus*) hatchlings. Large letters denote study area sections; alpha-numeric codes indicate ID (when designated) of nearest adult burrow.

analyses in Excel version 2003 (Microsoft Corp., Redmond, Washington, USA), with alpha set at 0.05. Results are reported as means ± 1 S.E.

RESULTS

Savannah River Site.—At hatching, individuals from the 2001 cohort had a mean CL of 47.5 \pm 0.6 mm and a mean weight of 29.2 \pm 0.8 g (N = 32). Hatchlings grew an average of 32.7 mm CL (0.153 \pm 0.011 mm/d) and gained 99.7 g (0.456 \pm 0.043 g/d) during captive head-starting, thus attaining 80.2 \pm 2.5 mm CL and mean body weight of 128.9 \pm 9.8 g just prior to release. Survivorship of head-started tortoises from hatching to time of release was 100%.

During four years of post-release monitoring, we recaptured 17 of the 32 head-started hatchlings. We recaptured head-started animals one to three times (mean = 1.6) for a total of 31 recaptures. Annual survivorship of the single cohort of head-started tortoises varied among years, was lowest in the first year post-release (53.1%), and ranged from 82.3–92.8% in the subsequent three years (Fig. 4). Cumulative survivorship of headstarted tortoises was a minimum of 37.5% for the first four years following release (corresponding to ages one to four). Only one head-started tortoise was confirmed dead; we found tortoise #225 depredated by a medium-sized mammal 14 July 2003 (397 days post-release).

We found two dead translocated juveniles (#9, 147) shortly following translocation (5–8 October 2001) and another (#93) on 1 March 2002 prior to removal of enclosure walls. Our trapping efforts resulted in 50 recaptures (26 captures prior to enclosure removal) of 28 of the 35 tortoises translocated as juveniles. Annual survivorship of translocated juveniles ranged from 57.1–81.3% (mean = 73.7%; Fig. 4). Cumulative survivorship for translocated juveniles during the first four years following release was a minimum of 28.6%. We never found 20 of the translocated juveniles following release. Too few data were available for us to

calculate age-specific survivorship for translocated juveniles. Annual survivorship did not vary among years ($F_{3,7} = 9.276$, P = 0.669) or between head-started hatchlings and translocated juveniles ($F_{1,7} = 10.128$, P = 0.641). Because we only had a single survival estimate for each treatment for each year, we could only test for main effects.

St. Catherines Island .- The mean CL of headstarted hatchlings from the 2005 cohort was 74.1 \pm 1.2 mm and mean weight was 84.9 \pm 2.8 g (N = 7) at time of release (13 June 2005; Fig. 5). The 2005 cohort gained an average of 48.1 g $(0.287 \pm 0.015 \text{ g/d})$ and had 100% survivorship during the captive head-starting period. Hatchlings from the 2006 cohort (N = 33) were 50.9 \pm 0.4 mm CL in size and weighed 34.0 \pm 0.9 g at hatching. The 2006 cohort grew an average of 16.6 mm CL $(0.094 \pm 0.005 \text{ mm/d})$ and gained 39.5 g $(0.229 \pm 0.016 \text{ g/d})$ during captive head-starting, attaining $67.5 \pm 1.0 \text{ mm CL}$ (Fig. 5) and mean body weight of 73.6 ± 3.0 g just prior to release (23 March 2007). Of the 2006 cohort, 97.0% survived the captive head-start period. The 2005 cohort was significantly larger (by an average 6.5 mm CL; t = 4.18, df = 17, P < 1000.001) and weighed significantly more (mean difference 11.3 g; t = 2.73, df = 21, P = 0.013) than the 2006 cohort at the end of the captive headstart period. The average size of the 2007 (N =92), 2008 (N = 30), and 2009 (N = 56) cohorts of direct-released hatchlings ranged from 48.2-51.6 mm CL and 33.0–36.7 g body weight. Daily increase in mass (g/d) was significantly higher in the SRS head-starts than in either the 2005 $(t = 3.73, df = 36, P \le 0.001)$ or the 2006 (t =5.06, df = 37, P < 0.001) SCI head-starts. Daily increase in size (mm/d CL) of SRS head-starts was also significantly higher than in the 2006 SCI head-starts (t = 4.62, df = 48, P < 0.001). Finally, daily increase in mass was significantly higher in the 2005 SCI cohort compared to the 2006 SCI cohort (t = 2.83, df = 18, *P* = 0.015).

We recaptured 56 released head-started and



FIGURE 4. Annual post-release survivorship of head-started hatchling (2001 cohort) and translocated juvenile (multiple cohorts, ages one to nine) Gopher Tortoises (*Gopherus polyphemus*) released on the Savannah River Site, South Carolina, USA.



■Hatching size ■Release size

FIGURE 5. Hatching size and release size for head-started (HS) and direct-released (DR) Gopher Tortoise (*Gopherus polyphemus*) hatchlings released on St. Catherines Island, Georgia, USA. Hatching size was not available for 2005 cohort. Sample size indicates number of animals successfully hatched from each cohort.



FIGURE 6. Cumulative survivorship of head-started (HS; dashed lines, filled markers) and direct-released (DR; solid lines, hollow markers) Gopher Tortoise (*Gopherus polyphemus*) hatchlings released on St. Catherines Island, Georgia, USA.

direct-released hatchlings during 2006-2010. The 2005 head-starts exhibited remarkable survivorship, with an annual survivorship of 100% and all seven tortoises surviving the first four years post-release (Fig. 6). In contrast, only one of the 32 released head-starts from the 2006 cohort was known to survive. All mortality apparently occurred within the first year following release; we directly confirmed mortality of most head-starts when we discovered their depredated shells within a few days following their release. Annual survivorship for the 2006 headstarted cohort was 3.1% during the first year postrelease and 100% for each of two subsequent years of monitoring, resulting in a cumulative survivorship of 3.1% for the first three years post-release. The two cohorts of direct-release hatchlings for which we have sufficient monitoring data (2008, 2009) experienced similar survivorship rates during their first year post-release: 20.0% and 28.6%, respectively (Fig. 6). All tortoises from the 2008 cohort known to survive their first year also survived their second year.

DISCUSSION

Although survivorship during captive headstarting was high for both sites, head-started hatchlings at the SRS grew more while in captivity,—both per day and over the entire head-start period. On average, hatchling carapace length increased by nearly 70% (32.7 mm) and weight increased by more than 300% during head-starting (128.9 g). At time of release, SRS head-started tortoises (8–9 mo old) were comparable in size (mean CL = 80.2 mm) to three year old wildcaught tortoises, based on data from south-central Alabama (range 75-101 mm CL, Aresco and Guyer 1999) and central Florida (range 55-99 mm CL, Mushinsky et al. 1994), while the SCI head-started tortoises (6-7 mo old) were approximately the size of two year old wild-recruited juveniles (48-73 mm CL [Mushinsky et al. 1994]; 66-74 mm CL [Aresco and Guyer 1999]) with mean proportional size and mass increases of 33 and 130% respectively. Furthermore, significant differences in release sizes were observed between the 2005 and 2006 SCI cohorts. The variation in growth observed among cohorts while in captivity is not due solely to the length of the head-starting period but is most likely a function of variation in hatchling feeding protocols, which were not standardized between sites or among years but varied due to personnel resources. However, based on qualitative observations, all headstarted tortoises appeared healthy and exhibited normal shell hardness without pyramiding of scutes on the shell during their time in captivity.

The first year of the life of a Gopher Tortoise is often associated with relatively low survivorship (Alford 1980; Morafka 1994). The highest survival rate reported in literature for free-ranging hatchlings was 90-100% surviving from hatching to their first winter, with 57.1% surviving through the end of their first winter in northern Florida (Butler et al. 1995; Butler and Sowell 1996). Most other studies have documented much lower survivorship rates for hatchlings prior to their first dormancy period (Epperson and Heise 2003; Pike and Seigel 2006). The three cohorts (one from SRS, two from SCI) of head-started hatchlings exhibited nearly 100% survivorship from hatching to first dormancy while in captivity, with only one 2006 SCI hatchling dying prior to release. Thus, based on our observations of pre-release survivorship during captivity, head-starting was effective in increasing survivorship through their first winter, which is an important consideration in the assessment of head-starting as a management tool.

For the SRS head-started hatchlings, postrelease survivorship was lowest the first year following release. The first year following release was also the only year in which headstarted hatchlings experienced lower survivorship (53.1%) than did translocated juveniles (80.0%), although this difference was not significant. Estimating survivorship using mark-recapture is challenging, especially when the species in question is small-bodied, cryptic, and rarely active, hence the survivorship values reported here are

minimums. Our estimations of survivorship during the first year post-release had the advantage of head-started hatchlings and translocated juveniles being confined to field enclosures where we could detect them, thus our survivorship estimates for first year post-release are closer to true survivorship. In contrast, the drop in apparent survivorship in translocated juveniles during the second year is most likely a function of dispersal of juveniles from the local release site and a decrease in their detectibility once enclosures were removed.

After the first year (and once enclosures were removed), post-release survivorship of SRS head-started hatchlings was consistently high (82.3-92.8% per year). Survivorship of headstarted hatchlings was at least as high as observed for translocated juveniles, even though the latter consisted of older cohorts. Unfortunately, there are few published data available for comparison with free-ranging juvenile Gopher Tortoises beyond the hatchling stage. Wilson (1991) radio-tracked 32 juveniles ages one to four for varying lengths of time over a one year period in west-central Florida. She reported bi-monthly survival rates, which varied seasonally. These bimonthly survival rates convert to an estimated annual survival rate of 45.4%. The only other published survivorship estimate for juveniles is based on long-term mark-recapture records for Gopher Tortoises translocated to SCI (Tuberville et al. 2008). Tortoises translocated as juveniles had 84% post-release annual survival, but this estimate was based on data for multiple cohorts and included captures of translocated juveniles after they reached maturity. Thus, SRS head-started tortoises exhibited survivorship twice the rate reported for wild-recruited juveniles of the same age and at least as high as documented for translocated juveniles that were in many cases older and larger.

Post-release survivorship of the 2005 cohort of SCI head-started tortoises was remarkable, with all seven individuals surviving the first four years after release. In contrast, only one individual (3.2%) from the 2006 cohort of SCI head- to occur shortly following release. Likewise, a started hatchlings was known to have survived until the first post-release dormancy period. Thus, although the 2005 head-starting effort at SCI was extremely successful, the similar 2006 headstarting effort failed to improve survival beyond levels expected for unmanipulated hatchlings. There are several possible explanations for the extremely low survival rate, including, but not limited to: (1) the smaller body size of the 2006 SCI cohort compared to the SRS cohort or the 2005 SCI cohort increased their vulnerability to predators or other mortality sources (O'Brien et al. 2005; but see Pike and Seigel 2007); (2) an increase in predator abundance or decrease in abundance of alternate prey on SCI between 2005-2006 resulted in higher predation rates (Esque et al. 2010); (3) predators developed a search image for hatchlings and were more successful in locating or depredating released hatchlings (Butler and Sowell 1996); or (4) differences in release procedures. Although one or more of the above factors may have played a role, in retrospect, we suspect that the low observed survivorship rate for the 2006 head-start cohort was due largely to poor release conditions. Survivorship of this cohort might have been higher if release conditions had been given more careful consideration.

In our study, head-started tortoises (SCI 2006 cohort only) were released late in the day (between 1400–1600), shortly before Raccoons (Procyon lotor) – the primary predator of young Gopher Tortoises at SCI and many other sites (Diemer 1986), would have become active (Greenwood 1982; Ladine 1997). Any hatchling that did not seek immediate shelter in a provided burrow or other refuge would have been vulnerable to predation. Indeed, staff revisited the release site during the first week following release and observed damaged shells of head-started hatchlings apparently depredated by raccoons. This observation confirms that failure to recapture most of the 2006 cohort was due primarily to mortality rather than dispersal and also provides supporting evidence that most mortality tends

recent retrospective analysis of extremely high predation rates on translocated Desert Tortoises (G. agassizii) revealed that the elevated mortality was most likely due to widespread climate conditions and predator-prey dynamics at the time of release rather than any effects of translocation manipulations (Esque et al. 2010).

Due to reduced availability of personnel and space for continued head-starting, the extremely low survival rate observed for the 2006 cohort, and lack of demonstrated need for head-starting or other manipulations to increase the resident population size at our study site, subsequent cohorts from SCI were not head-started. Instead, hatchlings were released into temporarily installed predator-proof cages shortly following hatching. Post-release survivorship of 2008 and 2009 direct-released SCI hatchlings through their first winter was 20.0% and 28.6%, respectively. Most previous studies of hatchlings employed radio-telemetry to monitor individuals following their release at the nest site and reported survival during the first 30 days and/or during first 365 days, making it difficult to make comparisons with our mark-recapture data. Epperson and Heise (2003) reported that only 13 of 48 (27.1%) of hatchlings in Mississippi survived through their first winter, which was similar to our findings. In contrast, Butler et al. (1995) reported eight of 14 (57.1%) hatchlings in northern Florida surviving their first winter.

The expected low, but highly variable annual survivorship of hatchlings observed in most studies, along with the small sample size and lack of an experimental control in our project, make it difficult to draw conclusions regarding the effectiveness of temporary enclosures in improving hatchling survival. In addition, differences in site-specific characteristics and stochastic events (e.g., habitat quality, predator communities, annual variation in weather conditions) hinder our ability to make comparisons of survivorship between SCI hatchlings and hatchlings in other studies. However, several

lines of evidence point to the potential utility of temporary enclosures. Most of the hatchling mortality documented in previous studies occurred within the first 30 days after hatching (Epperson and Heise 2003; Pike and Seigel 2006). Likewise, the dramatic predation event at SCI occurred within a few days after the 2006 cohort of head-started tortoises was released. Although subsequent cohorts of direct-released hatchlings at SCI experienced mortality after their temporary enclosures were removed, the fact that all post-release mortality apparently occurred sometime prior to or during their first dormancy suggests that leaving enclosures in place for longer might have further reduced mortality. Smith (1997) reported that 42.8% of hatchlings confined to a 30 m² predator-proof enclosure in north Florida survived to 280 days, compared to 7.7% of hatchlings that were not released into protective enclosures. More recent work in southwest Georgia demonstrated that large-scale predator exclosures were associated with higher Gopher Tortoise nest survival (66.4% vs. 34.9%), higher hatchling survival (74.4%) vs. 37.5%) and an increase in juvenile burrows when compared to unfenced control plots (Smith et al. 2013). Collectively, these studies provide further evidence that predation can have a strong influence on recruitment in at least some Gopher Tortoise populations.

Conclusions and Recommendations.—Here we report our observations on survivorship of manipulated Gopher Tortoise hatchlings, including individuals head-started in captivity through their first dormancy and individuals released into temporary predator-proof enclosures shortly after hatching. Although our study was not designed to test the effectiveness of these manipulations, several patterns emerged. First, for each cohort, the lowest survivorship rates occurred during the first year following release. This pattern is in keeping with previous studies reporting direct observations of low survivorship in hatchlings monitored using radio-telemetry (Butler and Sowell 1996; Epperson and Heise 2003; Pike and Seigel 2006) and indirect demographic evidence (e.g., burrow and/or tortoise size distributions) that survivorship in Gopher Tortoises is lowest in the first year of life (Alford 1980; Witz et al. 1992). Second, head-started hatchlings exhibited extremely high survivorship while in captivity and can potentially experience high post-release survivorship as well. Finally, post-release survivorship of manipulated hatchlings was highly variable. Although hatchling performance may have been directly influenced by our hatchling manipulations and release protocols, any such effects could not be separated from effects due to release site characteristics or annual variation in environmental conditions.

Nonetheless, based on our experiences and observations with head-starting and use of temporary predator-proof enclosures with hatchling Gopher Tortoises (including efforts described here and smaller-scale efforts associated with other projects), we recommend the following:

(1) When implementing head-starting or other hatchling manipulations, develop protocols that consider not only conditions while hatchlings are in captivity, but also desired criteria for release site selection and timing of releases (both time of day and time of year);

(2) If employing predator-proof enclosures, confine hatchlings at least until they initiate dormancy, even though that may require larger-scale enclosures than the ones used in our study;

(3) When possible, include an experimental component as part of the project design to allow critical evaluation of the effectiveness of manipulations;

(4) To reduce personnel requirements and minimize unintended physiological or behavioral modifications (e.g., surface activity and dormancy timing; Pedrono and Sarovy 2000) that could affect post-release performance of hatchlings, we recommend minimizing the intrusiveness of techniques (e.g., protect nests in situ rather than artificially incubate eggs, rear hatchlings in temporary in situ enclosures instead of head-starting indoors) and using less intrusive methods that are likely to be sufficiently effective (Seigel and Dodd 2000).

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