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Overwintering of Gopher Tortoises (*Gopherus polyphemus*) Translocated to the Northern Limit of Their Geographic Range: Temperatures, Timing, and Survival

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Abstract. – We examined overwintering behavior in gopher tortoises (*Gopherus polyphemus*) translocated to the northern periphery of their geographic range by using miniature temperature data loggers during 2 winters. All adult and juvenile tortoises monitored with temperature loggers survived overwintering; however, during the course of the study 2 translocated juvenile tortoises without temperature loggers died during winter months. Onset and termination of overwintering were not different between the 2 yrs and were not correlated with mean above-ground air temperature. Mean overwinter duration was 127 ± 9 d SD and 128 ± 13 d SD during 2002–2003 and 2004–2005, respectively. Tortoises experienced temperatures as low as 7°C and as high as 31°C while overwintering; however, most (12 of 15) tortoises experienced very little (< 1°C) mean daily temperature fluctuation despite air temperatures regularly dropping below 0°C and exceeding 20°C. The overall mean temperature of overwintering tortoises was 12.4° ± 0.8°C (2002–2003) and 12.6° ± 1.2°C (2004–2005). Large fluctuations in temperature occurred when tortoises actively basked, and half of the monitored tortoises did, particularly juveniles, which accounted for 42% of winter basking events. Our results suggest that, given timely access to suitable refugia at recipient sites, overwinter mortality of translocated adult individuals may be minimal.

Key Words. – Reptilia; Testudines; Testudinidae; thermal ecology; conservation; translocation; gopher tortoise: *Gopherus polyphemus*; iButtons; dormancy; overwintering

Translocation, defined by Griffith et al. (1989) as the intentional release of individuals of a species to establish, reestablish, or augment a population of that species, is becoming a more widespread management tool and, as such, has garnered rigorous debate (Burke 1991; Dodd and Seigel 1991; Reinert 1991; Germano and Bishop 2008). Although early translocation efforts primarily focused upon game species (e.g., Griffith et al. 1989; Wolf et al. 1996), many projects have recently focused on the translocation of reptiles (e.g., King et al. 2004; King and Stanford 2006; Field et al. 2007; Roe et al. 2010). Ethical animal translocation projects have conservation value when they result in the establishment of new viable populations or help augment depressed populations. Consequently, reptile translocation projects should involve postrelease monitoring to assess the achievement of these goals (Kingsbury and Attum 2009). Frequently, measures of survival and movement (i.e., site fidelity) of individuals are used as the basis for evaluating success (Burke 1991; Dodd and Seigel 1991; Plummer and Mills 2000; Tuberville et al. 2005; King and Stanford 2006; Tuberville et al. 2008); however, the thermal ecology of translocated reptiles, particularly during the overwintering period, has received little attention.

Winter mortality of reptile species in temperate climates can be high and can limit population size and geographic distribution (Ultsch 2006). Winter survival is often dependent upon the timely selection of proper overwintering refugia. Translocated reptiles may be at a distinct disadvantage when seeking suitable refugia because of their unfamiliarity with their new landscape and its local environmental conditions. As a result, overwintering mortality has been cited as the primary source of mortality for some translocation attempts (King et al. 2004). This phenomenon may be even more likely to adversely affect individuals translocated over large spatial scales where local conditions, although suitable, may be different from those to which they are accustomed. As such, the overwintering survival of translocated individuals may be a function of not only the suitability of the recipient site but also of the ability of individuals to locate and inhabit thermally suitable overwintering sites.

The gopher tortoise (*Gopherus polyphemus*) is the most frequently displaced reptile in the southeastern United States (Dodd and Seigel 1991), often to remove individuals from immediate developmental threats (i.e., relocation). Historically, the primary goal of most tortoise relocations has been to ensure the welfare of the individual rather than to establish viable populations, thus until recently (e.g., Heise and Epperson 2005; Tuberville et al. 2005; Ashton and Burke 2007) most projects have not included a postmovement monitoring component. There is evidence that reptile relocation projects to minimize or avoid human-wildlife conflicts have high rates of failure (Germano and Bishop 2008), which further highlights the need for thorough and well-designed monitoring of moved individuals. To the best

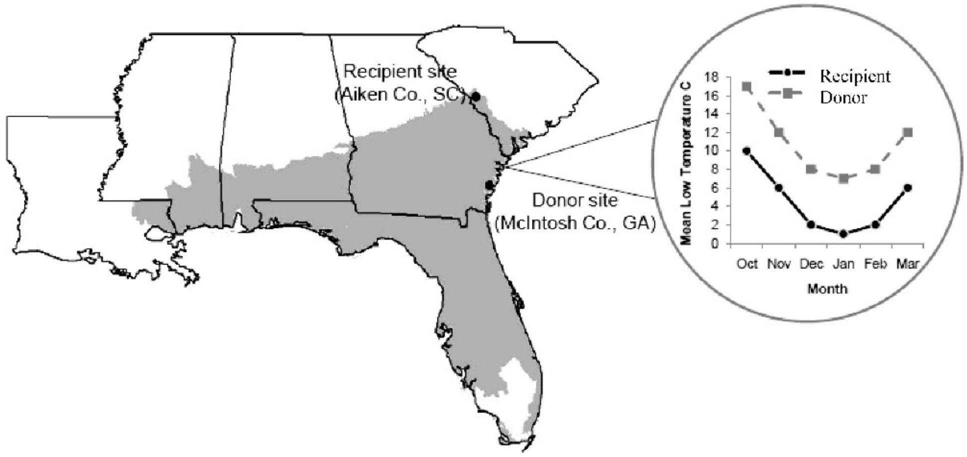

Figure 1. Map that illustrates the geographic distribution of the gopher tortoise (*Gopherus polyphemus*) and the locations of the donor and recipient sites for tortoises translocated as part of this project. The insert illustrates the local mean minimum air temperature reported for each site, with the recipient site (located 217 km north of the donor site) being colder in each of the winter months.

of our knowledge, no translocation or relocation study has monitored the overwintering ecology of displaced gopher tortoises despite the frequency at which populations of the species are moved.

In this study, we examined the timing, temperatures experienced, and survival of gopher tortoises translocated roughly 217 km to the northwest from their site of origin to a recipient site at the northern limit of the species' range. Our objectives were to 1) correlate the timing of overwintering with exogenous temperature cues, 2) examine the temperatures experienced and the thermal buffering of overwintering tortoises in their burrows, and 3) quantify overwintering mortality of tortoises following translocation.

METHODS

Study Site. — During August–October 2001, 106 gopher tortoises (39 adults, 32 juveniles, and 35 hatchlings) were translocated from a 40-ha industrial development site (donor site) in southeastern Georgia to a recipient study site on the Savannah River Site (SRS) in Aiken, South Carolina (Fig. 1; see Tuberville et al. 2005 for more details). The SRS is an 800-km^2 area owned by the US Department of Energy and managed by the US Forest Service. Although tortoises were once abundant in the region (Holbrook 1842), no populations were present on the SRS at the time of translocation.

The recipient site was an 882-ha timber management compartment composed primarily of longleaf pine (*Pinus palustris*) aged 50–60 yrs. The understory includes a mixed-oak (*Quercus* spp.) shrub and a diverse herbaceous layer. Management of the site is focused on improving conditions for the federally endangered red-cockaded woodpecker (*Picoides borealis*) and reestablishing wiregrass (*Aristida stricta*), a dominant understory species of the longleaf pine ecosystem (Aschenbach et al. 2010). The recipient site is treated with prescribed fire approximately every 3 yrs and was burned during late spring 2001. Some tortoises were released during October 2001, whereas others were held at an off-site holding facility and released during spring 2002 (see Tuberville et al. 2005 for more details on release procedures). The SRS is located approximately 217 km to the northwest of the donor site. Based on long-term weather data (obtained from www.weather.com, accessed on 15 February 2011), the mean minimum monthly air temperatures for the recipient site are consistently 6°–8°C lower than those for the donor site during the overwintering period (October–March) (Fig. 1).

Tortoise and Environmental Temperatures. — Twenty-one tortoises (18 adults and 3 juveniles) were equipped with miniature temperature data loggers (5.9 mm height × 17.4 mm diameter, 3.12 g, Thermochron iButtons product DS1922L-F51; Dallas Semiconductor, Dallas, TX) during the summers of 2002 and 2004. To minimize disturbance to translocated tortoises, iButtons were downloaded opportunistically. Thus, some temperature loggers became filled to capacity and stopped recording, which resulted in incomplete data for some tortoises. Because of the strong concordance that has been documented between carapace and body temperature in turtles (Congdon et al. 1989; Grayson and Dorcas 2004; Pittman and Dorcas 2009), data loggers were attached with epoxy to the anterior most vertebral scute. We programmed data loggers to record temperature every 2 hrs (i.e., bi-hourly) during the overwintering period. Temperature data loggers had a resolution of 0.2°C, accuracy of 0.5°C, and could store up to 2048 recordings.

Environmental air temperatures (i.e., daily mean, minimum, and maximum) were obtained from a NOAA weather station located nearby in Aiken, South Carolina (NOAA station: Aiken 5se 380074). We used correlation analysis to examine relationships between meteorological data (mean air temperature) and timing of overwinter onset (day of year [DOY]). To detect differences between years, we compared mean air temperature between the winters of 2002 and 2004 by using paired-samples *t*-tests.

Timing of Overwintering. — Onset, duration, and termination of overwintering were interpreted from graphs of bi-hourly body temperatures by locating the date when the amplitude of the daily fluctuations became noticeably reduced (dormancy onset) or increased (dormancy termination). We defined onset of overwintering as the date after which a tortoise did not emerge from its burrow for at least 7 d (loosely based on Bailey et al. 1995; Nussear et al. 2007). Similarly, the termination of overwintering was defined as the date when a tortoise emerged from its burrow to bask for portions of at least 7 consecutive days. Many tortoises emerged to bask on mild days during the overwintering period; however, isolated emergence events were not considered to indicate termination of overwintering unless they occurred for 7 consecutive days. We compared dates of onset and termination of the 2002–2003 and 2004–2005 seasons by using Mann-Whitney U-tests. If either date of onset or termination of overwintering could be determined from an individual's data logger, then it was included in analyses, even if the data logger was not functioning for the entire overwintering period.

We made several calculations based on temperatures experienced by individuals with functioning iButtons for the complete overwintering period. We defined mean overwinter temperature as the mean temperature of all measurements while an animal was overwintering, including any mid-winter basking events. We defined minimum temperature as the lowest temperature experienced by the animal at any time during the overwinter period and the maximum temperature as the highest temperature experienced by the animal at any time during the same period. For each tortoise, we calculated the degree of thermal buffering experienced by using the classes proposed by Nussear et al. (2007) for desert tortoises (*Gopherus agassizii*). Thermal buffering was defined as the degree to which the temperatures that tortoises were exposed to in their burrows (based on the iButtons attached to their carapaces) fluctuated from daily minimum to daily maximum. Tortoises that experienced less than 1°C difference between mean daily minimum and maximum were classified as extremely buffered. Tortoises that experienced moderate buffering had mean daily fluctuations in body temperature between 1°C and 2°C. Tortoises that experienced relatively weak buffering underwent a mean daily temperature fluctuation of > 2°C. All temperature data are presented as mean ± 1 standard deviation. Because so few juvenile tortoises were monitored (1 in 2002 and 2 in 2004) and the possible thermal differences between small and large tortoises (Wilson et al. 1994), they were not included in analyses. However, data summaries of temperatures, overwintering onset and termination, and overwintering duration of juveniles are presented in Table 1. To assess the impact of overwintering on gopher tortoise survival, we calculated

Table 1. Onset, termination and duration of overwintering in 15 translocated gopher tortoises (*Gopherus polyphemus*) on the Savannah River Site, Aiken Co, South Carolina, during the winters of 2002–2003 and 2004–2005. For each individual monitored, we also report sex, carapace length, mean, minimum, and maximum overwintering temperatures, number of overwinter emergences, and whether or not the tortoise survived the overwinter period.

Tortoise ID	Sex	Midline carapace length (mm)	Overwinter onset	Overwinter termination	Overwinter duration (days)	Mean overwinter temperature °C (± 1 SD)	Overwinter minimum temperature °C	Overwinter maximum temperature °C	Overwinter emergences	Survived?
2002–2003										
1	J	232	9 Nov	19 Mar	130	14.1 ± 4.6	11.5	30	1	Yes
7	M	261	31 Oct	19 Mar	139	11.9 ± 4.1	8	27.5	2	Yes
99	M	303	11 Nov	10 Mar	119	11.9 ± 3.9	8.5	21	0	Yes
118	M	245	30 Oct	20 Mar	140	12.9 ± 4.5	10.5	21	0	Yes
2004	M	293	11 Nov	10 Mar	128	12.2 ± 2.4	7.5	28	0	Yes
86	F	289	21 Nov	19 Mar	117	11.7 ± 4.5	9.5	15.5	0	Yes
3031	F	305	16 Nov	20 Mar	124	12.6 ± 2.8	10	19.5	0	Yes
2004–2005										
213	J	113	4 Nov	12 Mar	128	12.2 ± 2.4	7.5	28	5	Yes
223	J	113	6 Nov	22 Mar	136	11.6 ± 3.3	8	29	4	Yes
7	M	262	11 Nov	29 Mar	138	11.6 ± 2.7	7.5	26	2	Yes
63	M	272	5 Nov	25 Mar	140	14.5 ± 3.3	11.5	28	0	Yes
118	M	250	14 Nov	9 Mar	115	13.3 ± 4.5	10.5	29	1	Yes
60	F	287	23 Nov	13 Mar	110	11.6 ± 3.8	7	31	1	Yes
95	F	331	25 Nov	5 Mar	100	13.9 ± 4.1	9	27.5	7	Yes
98	F	307	9 Nov	23 Mar	134	12.4 ± 3.9	9.5	28	1	Yes

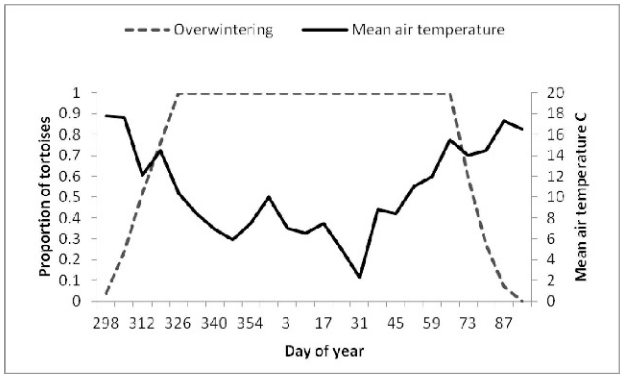

Figure 2. Proportion of translocated gopher tortoises (*Gopherus polyphemus*) entering and emerging from winter dormancy at the Savannah River Site, Aiken Co, South Carolina, in 2004–2005. Mean air temperature is also depicted, although the 2 variables were not correlated ($r = 0.44$, $F_{2,8} = 13$, $p = 0.28$).

the number of individuals that died during or shortly after winter dormancy, including both individuals monitored with iButtons and those which were not (total = 71). Hatchlings ($n = 35$) were excluded from analyses of overwinter survival as they were not monitored as intensively as adults and juveniles because of their small size and cryptic nature.

RESULTS

In 2002, 8 tortoises had functioning data loggers attached as they ceased aboveground activity and began to overwinter; 7 of those tortoises had functioning data loggers recording the entire duration of the overwintering period, including 1 juvenile tortoise. In 2004, 13 tortoises had data loggers attached as they began to overwinter; 8 of those data loggers recorded until the tortoise ceased dormancy in the spring, including 2 juvenile tortoises. Tortoises ceased aboveground activity over a 17-d period (30 October to 16 November) in 2002 and over a 19-d period (4 November to 23 November) in 2004 (Table 1). Tortoises ceased activity and entered burrows for the final time at a median date of 8 November (DOY = 312) during 2002 and 15 November (DOY = 319) during 2004. No statistical difference was detected between onset date for adult tortoises during the 2 winters (U = 39, $p = 0.27$). Although the dormancy onset period (25 October to 25 November) in 2004 had a higher mean temperature than 2002 (15.1° ± 2.0°C SD vs. 13.2° ± 1.1°C SD; $t = -2.26$, $p = 0.02$), mean air temperature was not correlated with date of overwintering onset during 2002 ($r = 0.32$, $F_{2,6} = 3.4$, $p = 0.36$) or 2004 (Fig. 2) ($r = 0.44$, $F_{2,8} = 13$, $p = 0.28$). Termination of dormancy for adults occurred over a 10-day period (10 to 20 March) during the spring of 2003 and over a 19-d period (10 to 29 March) in 2005. Median date of overwinter emergence of gopher tortoises in 2003 was 19 March (DOY = 78) and 20 March (DOY = 79) in 2005. No difference was detected between date of overwintering termination for the 2 yrs (U = 23, $p = 0.56$). Mean overwinter duration during 2002–2003 was 127 ± 9 d SD and was 128 ± 13 d SD for 2004–2005.

Mean temperature experienced by overwintering tortoises during the winter of 2002–2003 was 12.4° ± 0.8°C SD, with a minimum temperature of 7.5°C and a maximum of 30°C (Table 1). During the winter of 2004–2005, tortoises experienced a mean temperature of 12.6° ± 1.2°C SD, with a minimum of 7°C and maximum of 31°C. Of the 15 tortoises monitored for a complete dormancy season, 9 emerged at least once to bask during the dormancy period, which accounted for the highest recorded winter temperatures. The 3 juvenile tortoises we monitored with iButtons accounted for most of the observed basking events. During the winter of 2002–2003, the 1 juvenile we monitored accounted for 1 of the 3 observed basking events (33%), and, during 2004–2005, the 2 juveniles were responsible for 9 of 21 basking events (43%). In contrast, most adults emerged to bask on only 1 or 2 occasions during the overwinter period. Tortoises kept their body temperatures higher than air temperature minima and lower than air temperature maxima (Fig. 3) except when basking. During both winters, most tortoises adopted a strategy of extreme overwinter buffering with 5 of the 7 tortoises (including the juvenile) during the winter of 2002–2003 and 6 of the 8 (including 1 of the 2 juveniles) during 2004–2005, having a mean daily carapace temperature fluctuation of < 1°C. During each of the winters, 2 individuals, one of which was a juvenile (ID = 213), had a mean daily carapace temperature fluctuation between 1°C and 2°C (moderate buffering). None of the tortoises monitored experienced a mean temperature fluctuation more than 2°C while overwintering. Most of the observed variation in temperature experienced was due to isolated basking events in which tortoises briefly basked at the burrow entrance. Although air temperatures exceeded 20°C and dropped below 0°C, gopher tortoise temperatures typically remained stable between 9°C and 12°C (Fig. 3).

During the course of this study, all tortoises equipped with temperature loggers survived the overwintering period during which they were monitored. However, since initiating the postrelease monitoring of the translocated population (39 adults and 32 juveniles), we have documented 2 mortality events (2.8%) that may have been associated with overwintering. An immature tortoise (ID = 93, carapace length [CL] = 180 mm) released in fall 2001 without an iButton was found dead on 1 March 2002 and presumably perished overwinter, although it appeared healthy at time of release. In addition, an immature tortoise (ID = 81, CL = 205 mm) monitored via radiotelemetry as part of another study but not fitted with a temperature logger was known to be alive at onset of overwintering in the fall of 2003 but failed to emerge the following Spring. On 19 May 2004 a burrow camera was used to investigate the burrow and the carcass of the

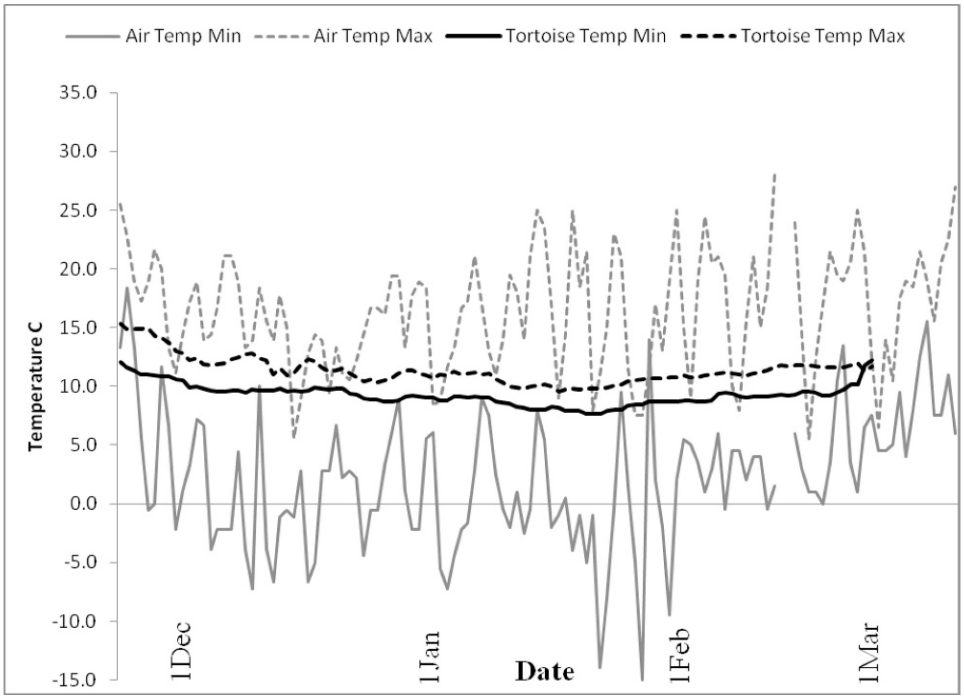

Figure 3. Mean carapace minimum and maximum temperatures of 6 overwintering translocated adult gopher tortoises (*Gopherus polyphemus*) relative to coincident air temperatures on the Savannah River Site, South Carolina, during the winter of 2002–2003. Five of the 6 tortoises were considered to have adopted a high thermal buffering strategy, as the mean daily difference between their minimum and maximum temperature was less than 1°C.

tortoise was discovered. This tortoise's body condition (wt/CL) had declined by 4.8% during 2001–2002 and by 10.0% during 2001–2003.

DISCUSSION

Tortoises in this study experienced relatively cold temperatures (7°C) likely owing to the study site's location at the northern periphery of the species' geographic range (Fig. 1). Although relatively few observations of temperatures experienced by overwintering gopher tortoises are available for comparison, the temperatures recorded in burrows during our study are colder (as low as 7°C) than minimums reported by Hubbard (1894; 23°C), Boulenger (1914; 21°C), or Einem and Ober (1956; 18°C). In fact, all tortoises monitored in this study experienced lower minimum (7°–11°C) and had lower mean (11.6°–14.1°C) temperatures than the minimum temperatures reported by the previously cited studies. Congdon et al. (1989) reported a similar mean overwintering temperature (12.3°C) for buried eastern box turtles (*Terrapene carolina*) at another study site on the SRS. Douglass and Layne (1978) showed that, although winter air temperature in Florida fluctuated from 21°C to 34°C, the temperature within tortoise burrows stayed relatively constant (26°–27°C). However, ours is the first study to continuously monitor the overwintering temperature and temperature fluctuations experienced by gopher tortoises. Most gopher tortoises experienced relatively little (mean < 1°C) daily temperature fluctuation while overwintering. When in their burrows, tortoise body temperatures were often warmer than air temperature lows and cooler than air temperature highs (Fig. 3). Air temperature fluctuated to a high degree both daily and seasonally, with temperatures exceeding 20°C and dropping below 0°C, with seemingly little effect on tortoise temperature. Semiaquatic turtle species that overwinter or aestivate terrestrially often occupy thermally buffered refugia to minimize daily temperature fluctuations (e.g., Buhlmann and Gibbons 2001). This thermally stable state is at least partially due to the extensive burrows that gopher tortoises excavate and inhabit (Carr 1952; Ultsch 2006). The closely related desert tortoise, whose burrows are not usually as extensive, typically experience a higher degree of mean daily temperature fluctuation (most between 1°C and 2°C but with some > 2°C) while hibernating (Nussear et al. 2007). It remains unclear to what degree the daily vertical movement of tortoises within their burrows contributes to their thermal stability.

The most extreme temperatures experienced were the highs by tortoises that actively basked. In more southerly parts of their range, aboveground tortoise activity has been documented in all 12 mo of the year (Douglass and Layne 1978; Butler et al. 1995), but the extent to which tortoises in more northerly locations exhibit surface activity in winter was poorly known. Nine of the 15 tortoises that we monitored emerged from their burrows to bask during the winter period, which accounted for 24 observed basking events (Table 1). All 3 juvenile tortoises that we monitored basked during the overwintering period, which accounted for 42% (33% in 2002–2003 and 43% in 2004–2005) of the observed basking events. Wilson et al. (1994) reported that juveniles basked on their burrow aprons more frequently in winter than in any other season. Overwinter basking behavior appears more prevalent in juvenile gopher (Butler et al. 1995; Diemer 1992) and desert tortoises (Wilson et al. 1999) than in adults, likely due to their faster heating and cooling rates (Wilson et al. 1994). One adult female tortoise (ID = 95) exhibited markedly different basking behavior compared with the other adults, emerging to bask 7 times during the 2004–2005 overwinter period, which accounted for 33% of that winter's observed basking events (Table 1). This tortoise accounted for the majority of observed overwintering basking events by adult tortoises.

None of the tortoises that we monitored with temperature data loggers died during the overwintering periods in which we monitored them. Of the 39 adult and 32 juvenile gopher tortoises translocated to our study site, only 2 juveniles were known to perish during the winter months, both without iButtons. Because these tortoises were translocated to the northern extent of their geographic range, presumably closer to their thermal threshold, this low mortality rate is surprising when considering the reported high failure rate of many translocation and relocation projects (reviewed in Dodd and Seigel 1991; Germano and Bishop 2008). Furthermore, both mortalities were of immature gopher tortoises, which typically have lower annual survival than adults, particularly during the late fall and early spring period (Wilson 1991). The high overwinter survival rate that we observed is likely due to the ability of tortoises to construct their own refugia and the thermal buffering provided by those burrows.

We documented variation among individual tortoises in the onset and termination date of winter dormancy (Table 1), although the median dates of both onset and termination were similar between years (median date of onset DOY = 312 [2002] and 319 [2004] and median date of termination DOY = 78 [2003] and 79 [2005]). Although no statistical difference in timing was detected between years, both onset and termination of dormancy occurred over the course of 19 d. In comparison with gopher tortoises at a site in Mississippi (the western periphery of the species' geographic range), tortoises on the SRS entered dormancy at a later median date (DOY 312 vs. 288), terminated dormancy earlier (DOY 78 vs. 114) and were dormant for shorter periods of time (128 vs. 188 days; Yager et al. 2007). Nussear et al. (2007) reported even larger variation in onset and termination of hibernation among desert tortoises, with individuals entering hibernation over the course of 44 d and emerging over as many as 49 d, although their sample sizes were larger and included tortoises from multiple study sites. We were unable to detect a relationship between onset of dormancy and air temperatures (Fig. 2). Likewise, Nussear et al. (2007) were unable to detect a relationship between onset of desert tortoise overwintering and air or soil temperatures. Further investigations will be needed before exogenous factors can be discarded as the drivers of dormancy timing as they are considered important factors that influence dormancy in other terrestrial turtle species (e.g., Grobman 1990; Bernstein and Black 2005).

Analysis of our results suggests that gopher tortoises translocated to the northern periphery of their geographic range experienced cooler overwintering temperatures than tortoises from more southerly locations (i.e., Georgia, Florida). Despite the cooler mean air temperatures, tortoises experience relatively little diel fluctuation in body temperature, likely resulting from the buffering of their burrows. Access for translocated gopher tortoises to thermally suitable refugia is likely to be an important factor in the success of translocation efforts and warrants consideration when recipient sites are chosen for translocation projects. Furthermore, the thermal ecology and winter activity of translocated individuals should be incorporated in posttranslocation monitoring. Although many aspects concerning translocation of gopher tortoises have yet to be investigated, our study presents preliminarily positive results, which indicated that, if released into suitable within-range habitat, gopher tortoises can successfully overwinter in their new location.

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LITERATURE CITED

Aschenbach, T.A., Foster, B.L., and Imm, D.W. The initial phase of a longleaf pine-wiregrass savannah restoration: species establishment and community responses. Restoration Ecology 18:762–771.

Ashton, K.G. and Burke, R.L. 2007. Long-term retention of a relocated population of gopher tortoise. Journal of Wildlife Management 71:783–787.

BAILEY, S.J., SCHWALBE, C.R., AND LOWE, C.H. 1995. Hibernaculum use by a population of desert tortoises (*Gopherus agassizii*) in the Sonoran Desert. Journal of Herpetology 29: 361–369.

BERNSTEIN, N.P. AND BLACK, R.W. 2005. Thermal environment of overwintering ornate box turtles, *Terrapene ornata ornata*, in Iowa. American Midland Naturalist 153:370–377.

BOULENGER, E.G. 1914. Reptiles and Batrachians. New York: E.P. Dutton, 140 pp.

BUHLMANN, K.A. AND GIBBONS, J.W. 2001. Terrestrial habitat use by aquatic turtles from a seasonally fluctuating wetland: implications for wetland conservation boundaries. Chelonian Conservation and Biology 4:2–13.

BURKE, R.L. 1991. Relocations, repatriations, and translocations of amphibians and reptiles: taking a broader view. Herpetologica 47:350–357.

BUTLER, J.R., BOWMAN, R.D., HULL, T.W., AND SOWELL, S. 1995. Movements and home range of hatchling and yearling gopher tortoises, *Gopherus polyphemus*. Chelonian Conservation and Biology 1:173–180.

CARR, A. 1952. Handbook of Turtles: The Turtles of the United States, Canada, and Baja California. New York: Cornell Univ. Press, 542 pp.

CONGDON, J.D., GATTEN, R.E., AND MORREALE, S.J. 1989. Overwintering activity of box turtles (*Terapene carolina*) in South Carolina. Journal of Herpetology 23:179–181.

DIEMER, J.E. 1992. Home range and movements of the tortoise *Gopherus polyphemus* in northern Florida. Journal of Herpetology 26:158–165.

DODD, C.K. AND SEIGEL, R.A. 1991. Relocation, repatriation, and translocation of amphibians and reptiles: are they conservation strategies that work? Herpetologica 47:336–350.

DOUGLASS, J.F. AND LAYNE, J.N. 1978. Activity and thermoregulation of the gopher tortoise (*Gopherus polyphemus*) in southern Florida. Herpetologica 34:359–374.

EINEM, G.E. AND OBER, L.D. 1956. The seasonal behavior of certain Floridian Salientia. Herpetologica 12:205–212.

FIELD, K.J., TRACY, C.R., MEDICA, P.A., MARLOW, R.W., AND CORN, P.S. 2007. Return to the wild: translocation as a tool in the conservation of the desert tortoise (*Gopherus agassizii*). Biological Conservation 136:232–242.

GERMANO, J.M. AND BISHOP, P.J. 2008. Suitability of amphibians and reptiles for translocation. Conservation Biology 23:7–15.

GRAYSON, K.L. AND DORCAS, M.E. 2004. Seasonal temperature variation in the eastern painted turtle (*Chrysemys picta*). Herpetologica 60:325–336.

GRIFFITH, B., SCOTT, J.M., CARPENTER, J.W., AND REED, C.W. 1989. Translocation as a species conservation tool: status and strategy. Science 4:476–480.

GROBMAN, A.B. 1990. The effect of soil temperatures on emergence from hibernation of *Terrapene carolina* and *T. ornata*. American Midland Naturalist 124:366–371.

HEISE, C.D. AND EPPERSON, D.M. 2005. Site fidelity and home range of relocated gopher tortoises in Mississippi. Applied Herpetology 2:171–186.

HOLBROOK, J.A. 1842. North American Herpetology. Reprinted by the Society for the Study of Amphibians and Reptiles 1976.

HUBBARD, H.G. 1894. The insect guests of the Florida land tortoise. Insect Life 6:302–315.

KING, R., BERG, C., AND HAY, B. 2004. A repatriation study of the eastern massasauga (*Sistrurus catenatus*) in Wisconsin. Herpetologica 60:429–437.

KING, R.B. AND STANFORD, K.M. 2006. Headstarting as a management tool: a case study of the plains garter snake. Herpetologica 62:282–292.

KINGSBURY, B.A. AND ATTUM, O. 2009. Conservation strategies: captive rearing, translocation, and repatriation. In: Mullin, S.J. and Seigel, R.A. (Eds.). Snakes Ecology and Conservation. New York: Cornell Univ. Press, pp. 201–220.

NUSSEAR, K.E., ESQUE, T.C., HAINES, D.F., AND TRACY, C.R. 2007. Desert tortoise hibernation: temperatures, timing, and environment. Copeia 2007:378–386.

PITTMAN, S.E. AND DORCAS, M.E. 2009. Movements, habitat use, and thermal ecology of an isolated population of bog turtles (*Glyptemys muhlenbergii*). Copeia 2009:781–790.

PLUMMER, M.V. AND MILLS, N.E. 2000. Spatial ecology and survivorship of resident and translocated hognose snakes (*Heterodon platirhinos*). Journal of Herpetology 34:565–575.

REINERT, H.K. 1991. Translocations as a conservation strategy for amphibians and reptiles: some comments, concerns, and observations. Herpetologica 47:357–363.

ROE, J.H., FRANK, M.R., GIBSON, S.E., ATTUM, O., AND KINGSBURY, B.A. 2010. No place like home: an experimental comparison of snake reintroduction strategies. Journal of Applied Ecology 47:1252–1264.

TUBERVILLE, T.D., CLARK, E.E., BUHLMANN, K.A., AND GIBBONS, J.W. 2005. Translocation as a conservation tool: site fidelity and movement of repatriated gopher tortoises (*Gopherus polyphemus*). Animal Conservation 8:349–358.

TUBERVILLE, T.D., NORTON, T.M., TODD, B., AND SPRATT, J.S. 2008. Long-term apparent survival of translocated gopher tortoises: a comparison of newly released and previously established animals. Biological Conservation 141:2690–2697.

ULTSCH, G.R. 2006. The ecology of overwintering among turtles: where turtles overwinter and its consequences. Biological Review 1:1–29.

WILSON, D.S. 1991. Estimates of survival for juvenile gopher tortoises, *Gopherus polyphemus*. Journal of Herpetology 25: 376–379.

WILSON, D.S., MORAFKA, D.J., TRACY, C.R., AND NAGY, K.A. 1999. Winter activity of juvenile desert tortoises (*Gopherus agassizii*) in the Mojave Desert. Journal of Herpetology 33: 496–501.

WILSON, D.S., MUSHINSKY, H.R., AND MCCOY, E.D. 1994. Home range, activity and use of burrows of juvenile gopher tortoises in central Florida. In: Bury, R.B. and Germano, D.J. (Eds.). Biology of North American Tortoises. Washington, DC: United States Department of the Interior, National Biological Survey, Fish and Wildlife Research Report 13, pp. 147–160.

WOLF, C.M., GRIFFITH, B., REED, C., AND TEMPLETON, S.A. 1996. Avian and mammalian translocations: update and reanalysis of 1987 survey data. Conservation Biology 10:1142–1154.

YAGER, L.Y., HINDERLITER, M.G., HEISE, C.D., AND EPPERSON, D.M. 2007. Gopher tortoise response to habitat management by prescribed burning. Journal of Wildlife Management 71: 428–434.

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