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Long-term apparent survival of translocated gopher tortoises: A comparison of newly released and previously established animals

Tracey D. Tuberville[a,*], *Terry M. Norton*[b], *Brian D. Todd*[a,1], *Jeffrey S. Spratt*[b,2]

[a]*Savannah River Ecology Lab, Drawer E, Aiken, SC 29802, USA*
[b]*St. Catherines Island Foundation, 182 Camellia Road, Midway, GA 31320, USA*

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ABSTRACT

Most turtle species require high adult survivorship to maintain stable populations. Translocations are often implemented to conserve turtle populations but may cause demographic disturbance as a result of increased mortality or dispersal of released animals. The gopher tortoise (*Gopherus polyphemus*) is one of the most frequently translocated turtle species. Short-term monitoring indicates that dispersal by released tortoises is common, but few long-term data are available to determine if losses of translocated animals continue for multiple years. We used 12 years of mark-recapture data to investigate long-term apparent survival of two groups of gopher tortoises translocated during separate periods to St. Catherines Island, Georgia, USA. We analyzed capture histories in program MARK to compare apparent survival of newly released tortoises and previously established translocated tortoises and also to determine whether apparent survival varied with sex or maturity. Apparent annual survival did not vary between adult males and females (0.98 ± 0.01), but was lower in sexually immature tortoises (0.84 ± 0.05). We documented a temporary reduction in apparent survival of newly released adult (0.75 ± 0.06) and immature tortoises (0.45 ± 0.26) during the first year after release that may be attributed in part to permanent dispersal. However, for both maturity classes, apparent survival of newly released tortoises was consistently high and matched that of previously established animals during the remainder of the study. Additional long-term studies of both translocated and naturally-occurring populations are needed to improve management of remaining tortoise populations.

1. Introduction

Turtles have life histories characterized by delayed sexual maturity, relatively low annual fecundity, high egg and hatchling mortality, long reproductive life span, and high adult survivorship (Moll, 1979; Wilbur and Morin, 1988; Iverson, 1991; but see Buhlmann, 1998). Although values for each trait vary among species and among populations within species,

* *Corresponding author*: Tel.: +1 803 725 5757; fax: +1 803 725 3309.
E-mail addresses: tracey.tuberville@gmail.com (T.D. Tuberville), tnmynahvet@aol.com (T.M. Norton), btodd@vt.edu (B.D. Todd), jspratt@tnc.org (J.S. Spratt).
1 Present address: Department of Fisheries and Wildlife Sciences, Virginia Polytechnic Institute and State University, 100 Cheatham Hall, Blacksburg, VA 24061-0321, USA.
2 Present address: The Nature Conservancy, P.O. Box 484, Darien, GA 31305, USA.
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individual populations appear to be constrained in their ability to withstand demographic disturbances (Congdon et al., 1993). In addition, turtle populations can be more sensitive to changes in some life history traits (e.g., adult survivorship, age at maturity) than others (e.g., nest success, hatchling survivorship; Frazer, 1992; Heppell et al., 1996; Heppell, 1998). For terrestrial and freshwater turtles, maintenance of stable populations appears to depend on high adult survival, with reported annual survival rates typically >80% but as high as 90–98% in many species (see summary table in Iverson, 1991). Chronic disturbances that increase adult mortality – such as intentional harvest (Congdon et al., 1993, 1994; Reed et al., 2005), incidental by-catch (Hoyle and Gibbons, 2000; Dorcas et al., 2007), or road mortality (Gibbs and Shriver, 2002) – cannot be sustained by most long-lived turtle species (but see Fordham et al., 2007, 2008 regarding *Chelodina rugosa*).

Even short-term increases in adult mortality can potentially affect population stability. For example, a population of flattened musk turtles (*Sternotherus depressus*) in Alabama experienced a brief disease outbreak during which bi-weekly survival briefly dropped from 98–99% to 82–88% for a single month before returning to 96–99% (Fonnesbeck and Dodd, 2003). The population had declined by 50% within a year (Dodd, 1988) and still had not recovered to pre-disease abundance a decade later (Bailey and Guyer, 1998). Other sources of short-term adult mortality reported for turtle populations include drought (*Gopherus agassizii*; Longshore et al., 2003), habitat disturbance (*Terrapene carolina*, Dodd et al., 2006; *Testudo hermanni*, Stubbs et al., 1985) and changes in predator abundance or behavior (*Chelydra serpentina*; Brooks et al., 1991).

Not all short-term losses of adult turtles result in long-term population declines. High drought-related mortality has been documented for adult desert tortoises at sites with low forage abundance or unpredictable resource availability (Longshore et al., 2003). Longshore et al. (2003) concluded that the desert tortoise population at the poor quality site was able to persist due to immigration of tortoises from surrounding source populations in more productive habitats. Germano and Joyner (1988) attribute recovery of another population of desert tortoises from a short period of high adult mortality to immigration of new animals into the population and high juvenile growth and survival. Dodd et al. (2006) reported higher than normal mortality of box turtles (*T. carolina*) immediately following habitat disturbance, but determined that disturbance effects on the population were short-lived and did not result in long-term demographic consequences. Whether disturbances that cause increased losses of adult turtles will affect long-term population stability appears to be influenced by the length and severity of the disturbance, how long survival is affected once the source of the disturbance is removed, the abundance of juveniles for recruitment into the adult stage, and whether affected populations are isolated from surrounding populations.

Translocations, although they are typically implemented to achieve conservation objectives (e.g., establishing or augmenting populations), can be considered perturbations to focal populations (Sarrazin and Barbault, 1996). If large numbers of released animals are lost through mortality or dispersal, or if even small losses are sustained for many years, translocations could even be considered catastrophic events from which turtle populations must recover. Tortoises, particularly gopher tortoises (*Gopherus polyphemus*) and desert tortoises (*G. agassizii*), have been the subjects of numerous translocations. Short-term monitoring (usually 1–2 years) of translocated populations indicates that some adults are usually lost from the founder population as a result of dispersal (Doonan, 1986; Burke, 1989; Heise and Epperson, 2005; Tuberville et al., 2005). Ultimately, loss of newly translocated individuals – whether from dispersal or mortality – causes reductions in apparent survival, a term used to describe the proportion of animals remaining in a population within a user-defined area. Few long-term data are available to determine whether tortoise losses are restricted to the period immediately following translocation or whether losses are sustained for multiple years (Seigel and Dodd, 2000; but see Ashton and Burke, 2007). We used data from a 12-year mark-recapture study of translocated gopher tortoises to answer the following questions: (1) Does apparent survival vary between previously established tortoises and animals newly released into the same area? (2) Does apparent survival of newly released animals change over time? (3) Does apparent survival vary with sex or reproductive maturity?

2. Materials and methods

2.1. Study site and study population

Our study was conducted on St. Catherines Island, a privately owned barrier island 6.4 km off the coast of Liberty County, Georgia, USA. The 5670 ha island is approximately 16 km long and 3.2–4.8 km wide. The study site is a 162 ha pasture at the north end of the island that was created for cattle grazing in 1950 (Thomas et al., 1978) and planted with Bermuda grass (*Cynodon* sp.), spangle grass (*Chasmanthium latifolium*), and broomsedge (*Andropogon* sp.). Although cattle grazing was discontinued in 1982, the open habitat is maintained by mowing, resulting in a savanna-like grassland with a scarce overstory of longleaf (*Pinus palustris*), slash (*P. elliottii*), and loblolly (*P. taeda*) pines (Thomas et al., 1978). The pasture was burned in 1989. The pasture constitutes <3% of the island (Fig. 1) and represents the primary area of suitable habitat for tortoises on the northern half of the island.

Although the adjacent mainland is within the geographic range of the species, gopher tortoises (*G. polyphemus*) are not native to St. Catherines Island. Approximately 25–30 tortoises were released on the island between 1987 and 1993, but these tortoises, hereafter referred to as established tortoises, were not permanently marked prior to release and the wild population from which each individual originated is unknown. In Spring 1994, a population of 74 gopher tortoises (23 males [235–345 mm CL], 32 females [217–335 mm CL], and 19 immature tortoises [53–205 mm CL]) was translocated to St. Catherines Island from a development site in Bulloch County, Georgia. These tortoises, hereafter referred to as newly released tortoises, were permanently marked prior to release and were provided manually dug starter burrows.

A mark-recapture study was initiated in Spring 1994 to monitor newly released tortoises and to catalogue previously established tortoises present on the island. Subsequent bi-annual trapping was conducted each fall and spring from Fall

Fig. 1 – Map depicting the location and relative size of the study area on St. Catherines Island, Georgia, USA.

1994 to Spring 1998. No sampling occurred in 1999 or 2000; annual spring sampling resumed in 2001–2006. Spring sampling occurred primarily during May–June, and Fall sampling in September–October, although exact timing, duration and trapping effort varied among years. Trapping was conducted using bucket traps, except during Fall 1994 when established tortoises were manually extracted from their burrows with a pulling hook (Taylor, 1982) and during 2006, when wire live traps (Burke and Cox, 1988) were used in addition to bucket traps. Bucket traps consisted of 18.9-L plastic buckets buried at the entrance of tortoise burrows, covered with heavy duty paper, and disguised with sand (Burke and Cox, 1988) so that they were not visible to tortoises occupying burrows targeted for trapping. Sampling effort focused on recapturing tortoises released on the island with less emphasis placed on capturing tortoises recruited into the population as a result of on-island reproduction. The study area was periodically searched for new burrows, which were subsequently targeted for trapping. Because most suitable habitat in the vicinity of tortoise release sites occurred only in the study area, other less suitable areas of the island were not routinely searched for burrows or tortoises.

On initial capture (or first recapture for established tortoises), tortoises were permanently marked by filing notches in unique combinations of marginal scutes (Cagle, 1939) and most were also injected in the inguinal region or intramuscularly in an anterior leg with an electronic transponder chip (Trovan Electronic Identification Devices Ltd.). Mass to the nearest g and mid-line carapace length (CL) to the nearest mm were also recorded. Mature tortoises with concave plastrons and elongated gular scutes were classified as males. Tortoises that lacked secondary sexual characteristics were classified as females if CL was at least 220 mm; smaller tortoises were classified as immature. Because most tortoises were initially captured as reproductively mature adults, annuli counts could not be used to accurately age all individuals.

Based on health screening for upper respiratory tract disease (URTD; Brown et al., 2002), 80% of newly released tortoises tested positive for exposure to *Mycoplasma agassizii* when released in 1994. All newly released tortoises recaptured in 2004 ($n = 21$) tested positive for exposure to *Mycoplasma*, and in 50% of those tortoises, *Mycoplasma* was directly cultured from nasal wash samples using polymerase chain reaction (Norton and Spratt, unpublished data). However, no tortoise exhibited clinical symptoms of URTD during the study and the population appears very healthy based on long-term health evaluations.

2.2. *Demographic analysis*

We used capture history data collected from 1994–2006 to estimate annual apparent survival rates (Φ) and recapture probabilities (p) of tortoises. At least one previous study has identified increased precision and no bias in parameter estimates of long-lived tortoises if the recapture duration assumption is relaxed and the recapture period lengthened (O'Brien et al., 2005), especially if recapture probabilities remain above 0.2. Consequently, in years in which fall sampling periods were conducted 2–3 months after the late-spring sampling, we combined captures into one sampling period. Our sampling intervals for the mark-recapture analysis were thus annual.

We grouped animals into the following six categories depending on time of release, stage (maturity), and sex: (1) established immature tortoises, (2) established mature males, (3) established mature females, (4) newly released immature tortoises, (5) newly released mature males, and (6) newly released mature females, where "established" refers to tortoises released before 1994 and "newly released" refers to tortoises released into the study area in 1994. Immature tortoises included non-reproductive subadults and younger juveniles whose sex could not be determined. Hatchling gopher tortoises are infrequently encountered in field studies (Morafka, 1994) and we excluded the five hatchlings captured during the 12 years of data collection because four of them were never recaptured and the fifth was only recaptured once. All newly released tortoises in 1994 were known to be alive and were treated as captured for that year in their encounter histories.

We used a standard Cormack–Jolly–Seber (CJS) open population model to generate parameter estimates and to test hypotheses about the data. Sampling effort (e.g., total search hours, number of traps or volunteers) was not recorded during the study but was known to vary in some years. Thus, all candidate models include time-varying recapture probabilities but we could not explicitly model recapture probabilities as a function of sampling effort. We used program MARK (White and Burnham, 1999) to fit various CJS models to the data, starting with the most comprehensive "global" model that included time-varying effects for release group, reproductive stage, and sex group on both apparent survival, Φ, and recapture probability, p (Table 1). We subsequently eliminated factors from the global model one at a time to determine which were most important. We used Akaike's

Table 1 – Candidate Cormack–Jolly–Seber models used to estimate survival and recapture probability of tortoises

Model	AICc	Δ AICc	AICc weights	# Estimated parameters
Φ(stage + release-effect-year 1 * •)p(stage * t)	783.6	0.0	0.87	19
Φ(stage + release-effect-years 1 and 2 * •)p(stage * t)	787.3	3.7	0.13	21
Φ(stage * t)p(stage * t)	819.9	36.3	0	34
Φ(stage * •)p(stage * t)	823.0	39.5	0	22
Φ(group * t)p(stage * t)	826.1	42.5	0	39
Φ(stage + group * t)p(stage * t)	842.9	59.3	0	52
Φ(t)p(t)	846.0	62.5	0	19
Φ(sex + stage + group * t)p(stage * t)	898.7	115.1	0	73
Φ(sex + stage + group * t)p(t)	913.8	130.3	0	69
Φ(sex + stage + group * t)p(group * t)	930.1	146.5	0	79
Φ(sex + stage + group * t)p(stage + group * t)	934.3	150.8	0	89
Φ(sex + stage + group * t)p(sex + stage + group * t) GLOBAL MODEL	979.7	196.2	0	105

Candidate models were evaluated using Akaike's information criterion and are ranked here with the most parsimonious model at the top. Models included possible maturity effects (stage), sex effects (sex), release group effects (group), time-varying probabilities (*t*), or constant probabilities among years (•). Additionally, a possible short-term release effect on apparent survival (Φ) was modeled the first year or first two years after release.

information criterion (AIC) to evaluate relative support for candidate models and identify the most parsimonious model (Akaike, 1973; Burnham and Anderson, 2002). Finally, we modified the most parsimonious model to test for a temporary release effect on apparent survival of newly released tortoises in the first one or two years following their release into the study population in 1994. We present model averaged parameter estimates with unconditional standard errors using all our candidate models to generate weighted averages. We used Program RELEASE to test the overall fit of the global model to the data.

3. Results

3.1. *Mark-recapture summary*

The number of tortoises captured each year varied from a low of 7 tortoises captured in 2003 to a high of 50 captured in 1998 (mean = 29.9 per year, not including 11 established tortoises captured in 1994). Of the 76 newly released animals, several were never recaptured whereas others were recaptured during as many as 8 sampling periods subsequent to their release for a total of 9 observations (Fig. 2). The mean number of times a newly released tortoise was observed, including initial release observations, was 3.9 (range = 1–9; mean adult = 5.0; mean immature tortoise = 2.0; Fig. 2). Seventy-eight percent of adult tortoises newly released in 1994 were recaptured whereas only 37% of immature tortoises newly released in 1994 were ever recaptured. A total of 28 tortoises newly released in 1994 (11 adults, 17 immature) were never recaptured (Fig. 2). The maximum interval between release and first recapture for any newly released tortoise was 12 years for one adult male and the second longest interval between observations was 4 years.

Established tortoises that had been released prior to 1994 were observed an average of 3.8 times (range 1–9; mean adult = 4.2; mean immature tortoise = 3.4; Fig. 2). Because detailed records of tortoise releases and sightings were not kept prior to 1994, we do not know exactly how many tortoises released prior to 1994 were never sighted again. However, 11

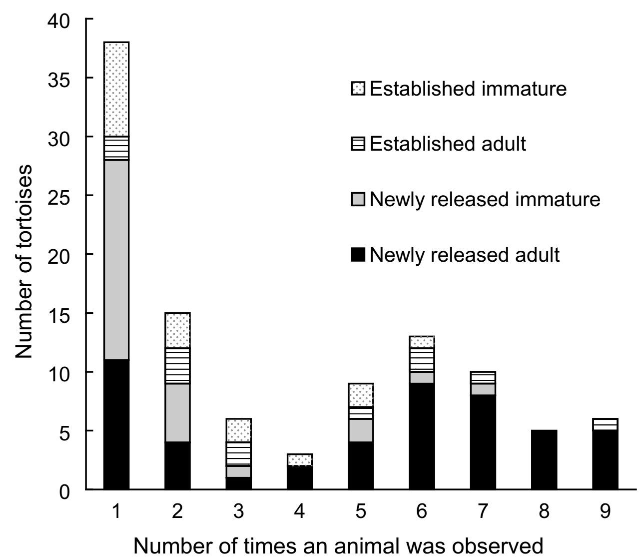

Fig. 2 – Frequency histogram showing the number of tortoises in categories based on the total number of times they were observed in 10 sampling years from the 12-year study. Observations include captures (or first releases for animals newly released in 1994) and recaptures.

established tortoises were recaptured during the first year of the mark-recapture study in 1994. The maximum interval between initiation of the mark-recapture study and first capture of a previously established tortoise was 12 years. The longest interval between captures of previously established tortoises was 10 years for an immature tortoise. Adults were recaptured more frequently than were immature tortoises regardless of whether they were released into the study site before 1994 or not (Fig. 2).

3.2. *Demographic analysis*

Goodness-of-fit tests using program RELEASE revealed that the global model adequately fit the data (combined TESTS 2 and 3: $\chi^2 = 33.5$, df = 33, $p = 0.44$). The model selection procedure revealed little support for candidate models in which recapture probability varied between the sexes or between release groups (prior to 1994 or after; Table 1). However, stage was found to be an important factor affecting recapture probabilities, with models that incorporated stage in recapture probabilities performing significantly better than comparable models that did not (e.g., ΔAIC > 10; Table 1). Similarly, we found little support for effects of sex or release group on apparent survival compared with otherwise identical candidate models that excluded these factors (Table 1). The two most parsimonious models (prior to inclusion of a short-term release effect on survival) found only stage to be an important factor in apparent survival and recapture probabilities, with time-varying apparent survival being favored over constant survival (ΔAIC = 3.1). Inclusion of a short-term release effect on apparent survival of newly released tortoises proved to be the most parsimonious fit, particularly for the model in which the release effect on apparent survival only manifested in the first year rather than the first two years (Table 1).

Model-averaged estimates of apparent survival and recapture probabilities with unconditional standard errors were calculated based on model weights of all candidate models. Average adult recapture probability was 0.53 ± 0.06 but varied among years, likely depending on sampling effort as well as any underlying biological mechanisms. Adult recapture probabilities during the course of the study ranged from a low of 0.14 ± 0.05 in 2003 to a high of 0.91 ± 0.04 in 1998 (Fig. 3). Average recapture probability of immature tortoises was 0.28 ± 0.09 and also varied among years. Recapture probability of immature tortoises was 0 ± 0.01 in many years in which none were captured and was as high as 1.0 ± 0.01 in a year in which, ostensibly, all immature tortoises were recaptured (Fig. 3). The next greatest recapture probability of immature tortoises was 0.51 ± 0.18 in 1997 (Fig. 3).

Apparent annual survival for adult tortoises averaged 0.98 ± 0.01 for all years excluding the first two (Fig. 4). Apparent survival of adults newly released in 1994 was 0.75 ± 0.06 in the first year but approached that of previously established adults in the second year (Fig. 4). Survival of immature tortoises was lower than that of adults and averaged 0.84 ± 0.05 across years. Again, however, a short-term release effect was seen in newly released immature tortoises in which apparent survival was 0.45 ± 0.26 in the first year and increased to 0.79 ± 0.2 in the second year (Fig. 4).

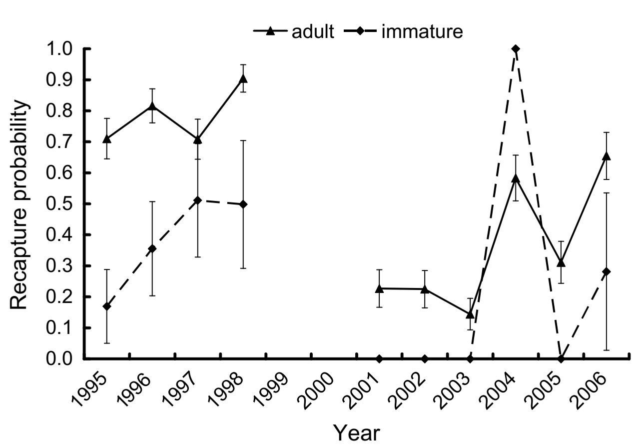

Fig. 3 – Model-averaged estimates of recapture probability (±SE) for adult and immature tortoises during each year of the study in which sampling was conducted. No sampling was conducted during 1999–2000.

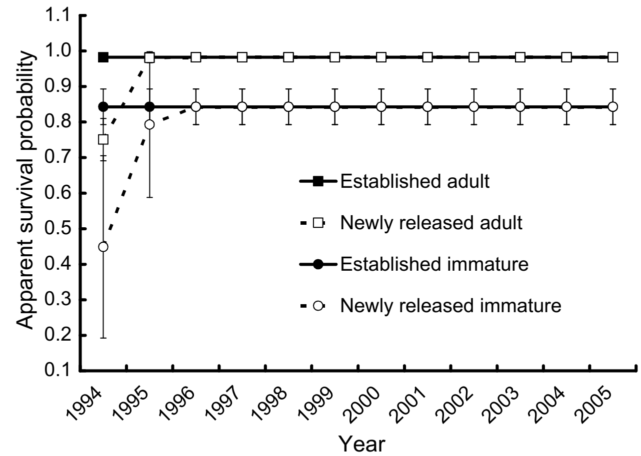

Fig. 4 – Model-averaged estimates of annual apparent survival (±SE) for tortoises from four groups at St. Catherines Island, Georgia, USA.

4. Discussion

Although more than 25,000 gopher tortoises were legally displaced as a result of development-driven habitat destruction in Florida during the 1990s alone (Enge et al., 2002), data from long-term monitoring of displaced populations are lacking (but see Ashton and Burke, 2007). Empirical data are crucial for evaluating whether translocation can be used effectively to manage gopher tortoise populations. Cox (1989) recognized that models for evaluating viability of translocated tortoise populations would need to consider any behavioral or demographic responses (such as dispersal) of tortoises to translocation. Seigel and Dodd (2000) were the first to develop a population viability model that explicitly considered potential behavioral or demographic responses (such as dispersal) of tortoises to translocation. They varied adult survivorship to reflect the anticipated loss of adults due to post-translocation dispersal and concluded that annual retention rates of at least 90% would be necessary to maintain a viable population. However, their model assumed retention rates would remain constant following translocation rather than increase over time.

Several studies have used radio-telemetry to monitor the short-term fate of adult translocated gopher tortoises (Doonan, 1986; Heise and Epperson, 2005; Tuberville et al., 2005). Altogether, these studies indicate that individuals are lost from the population primarily through dispersal from the release site rather than from direct mortality, with site fidelity during the first year ranging from 31% without prior penning (i.e., hard release) to 69–92% with prior penning (soft release). Field et al. (2007) reported high post-translocation mortality of telemetered desert tortoises but attributed the mortality to drought conditions rather than the translocation itself. A consistent observation among studies is that dispersal is typically confined to the first few weeks following release, demonstrating that the effects of translocation on tortoise behavior are apparently short-lived. Presumably, movement patterns eventually stabilize such that translocated tortoises subsequently exhibit site fidelity comparable to native, undisturbed tortoises.

Based on long-term monitoring of tortoises introduced to St. Catherines Island, apparent annual survival of tortoises released before 1994 was consistently high, averaging 0.98. The study area in which tortoises were released and subsequently sampled represented only a small portion of the island's entire area (<3%). Therefore, we do not think the high apparent survival of tortoises observed in our study was a function of the tortoises being artificially confined to the study area. In fact, limited monitoring of selected individuals via radio-telemetry demonstrated that newly released tortoises may disperse up to 3 km from their point of release (J. Spratt, unpublished data). The consistently high apparent survival of animals released prior to 1994 suggests that they had established residency by the time our study began and additional animals were introduced.

We observed a short-term release effect on apparent survival of both immature and adult tortoises newly released into the study area in 1994. During the first year, apparent annual survival of newly released adult and immature tortoises was significantly lower than that of previously established tortoises. Survival of newly released adult and immature tortoises increased in the second year and matched that of previously established tortoises for the remainder of the 12 year study. Based on aforementioned radio-telemetry studies of translocated tortoises, we attribute the short-term reduction of apparent survival of newly released tortoises mostly to permanent dispersal of newly released tortoises from the release area. Our findings mirror results from Ashton and Burke (2007), the only other published study of long-term site fidelity of translocated gopher tortoises. They reported post-translocation retention rates of 73% in year one, 92% in year two, and an annual average of 98.5% over the subsequent 15 years leading up to the resurvey.

How well our reported values for long-term survival of translocated tortoises on St. Catherines Island compare to survival of gopher tortoises from naturally-occurring populations is unknown. Unfortunately, there are no published estimates of long-term mortality or dispersal rates for natural populations. Mortality events due to disease have been reported (Gates et al., 2002; Seigel et al., 2003), but reference values for healthy populations are unavailable. Dispersal appears to be a rare event, is difficult to document in short-term studies, and is not well-quantified for naturally-occurring populations. Based on a one year telemetry study of 123 tortoises, Eubanks et al. (2003) documented dispersal of 2% of adults in unfragmented, high-quality habitat. Despite the paucity of available survival and dispersal data, it seems unlikely that tortoises in naturally-occurring populations could maintain much higher long-term apparent survival than the 98% per year reported here and by Ashton and Burke (2007). We suspect that when data become available, survival rates of naturally-occurring populations will be similar to long-term rates observed for gopher tortoises translocated to protected areas.

We did not observe a difference in apparent survival between adult male and adult female tortoises, but annual survival differed significantly between immature (0.84) and adult tortoises (0.98). Although immature tortoises may have smaller home ranges or exhibit higher site fidelity than adults following release (Berry, 1986; Tuberville et al., 2005), because of their smaller size and sometimes softer shells they are vulnerable to a wider array of predators. Immature tortoises are also difficult to effectively sample because their small, cryptic burrows are difficult to find, as illustrated in our study by the lower capture probability for immature tortoises (0.28) compared to adults (0.53). Few comparative data on survivorship of immature gopher tortoises (other than hatchlings, the 5 of which were excluded from our analysis) are available, but range from 45% (Wilson, 1991) to >80% (Tuberville and Buhlmann, unpublished data). Both estimates are based on short-term studies, so the wide range in values may reflect year-to-year variation in survival. Our 12-year study at St. Catherines provides a long-term estimate of apparent survival in immature gopher tortoises that was previously lacking for this species.

Our findings document an immediate short-term reduction in apparent survival of newly released tortoises relative to previously established translocated tortoises, which we attribute mostly to permanent dispersal of newly released tortoises from the study area. By the end of the first year, apparent annual survival of newly released tortoises corresponds with that of established tortoises, is consistently high through the remainder of the study, and is similar to values reported for another translocated population (Ashton and Burke, 2007). Long-term apparent survival of both newly released tortoises and previously established translocated tortoises exceeds the minimum estimate required to maintain viable populations of gopher tortoises (90%; Seigel and Dodd, 2000), the closely related desert tortoise (95%; USFWS, 1994), and the ploughshare tortoise (*Geochelone yniphora*, 95%; Pedrono et al., 2004), suggesting that translocation may be a potentially useful management tool for maintaining or establishing viable populations of tortoises. However, multiple population processes, including recruitment, need to be evaluated in order to determine if individual translocated populations are viable (Tuberville, 2008). Without data on reproductive success and tortoise recruitment the population viability of the tortoise population on St. Catherines Island is uncertain.

One of the primary impediments to effectively managing populations of gopher tortoises and other rare turtles is a lack of comprehensive life history data. Although the 12 year duration represents less than half the species' generation time (FFWCC, 2002), our study provides estimates of long-term survivorship of immature and adult gopher tortoises—estimates which have not been well-documented in the literature. Long-term studies of both translocated and naturally-occurring tortoise populations are needed to better understand survivorship and other life history traits and how they may vary among life stages, among years in response to fluctuating environmental conditions, and among sites as a result of local habitat conditions. A better understanding of the life history of gopher tortoises is required to provide effective long-term management of remaining populations, particularly when manipulations such as translocation or augmentation are implemented.

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REFERENCES

Akaike, H., 1973. Information theory and an extension of the maximum likelihood principle. In: Petrov, B.N., Cazakil, F. (Eds.), International Symposium Information Theory, second ed. Akademiai Kidao, Budapest, Hungary, pp. 267–281.

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

Bailey, K.A., Guyer, C., 1998. Demography and population status of the flattened musk turtle, *Sternotherus depressus*, in the Black Warrior River Basin of Alabama. Chelonian Conservation and Biology 3, 77–83.

Berry, K.H., 1986. Desert tortoise *Gopherus agassizii* relocation: implications of social behavior and movements. Herpetologica 42, 113–125.

Brooks, R.J., Brown, G.P., Galbraith, D.A., 1991. Effects of sudden increase in natural mortality of adults on a population of the common snapping turtle (*Chelydra serpentina*). Canadian Journal of Zoology 69, 1314–1320.

Brown, D.R., Schumacher, I.M., McLaughlin, G.S., Wendland, L.D., Brown, M.B., Klein, P.A., Jacobson, E.R., 2002. Application of diagnostic tests for Mycoplasmal infections of desert and gopher tortoises, with management recommendations. Chelonian Conservation and Biology 4, 497–507.

Buhlmann, K.A., 1998. Ecology, terrestrial habitat use, and conservation of a freshwater turtle assemblage inhabiting a seasonally fluctuating wetland with emphasis on the life history of *Deirochelys reticularia*. Dissertation. University of Georgia, Athens, GA

Burke, R.L., 1989. Florida gopher tortoise relocation: overview and case study. Biological Conservation 48, 295–309.

Burke, R.L., Cox, J., 1988. Evaluation and review of field techniques used to study and manage gopher tortoises. In: Szaro, R.C., Severson, K.E., Patton, D.R. (Eds.), Management of Amphibians, Reptiles, and Small Mammals in North America, 19–21 July 1988. US Department of Agriculture Forest Service, Flagstaff, Arizona, pp. 205–215.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information–Theoretic Approach. Springer-Verlag, New York, NY.

Cagle, F.R., 1939. A system of marking turtles for future identification. Copeia 1939, 170–173.

Congdon, J.D., Dunham, A.E., Van Loben Sels, R.C., 1993. Delayed sexual maturity and demographics of Blanding's turtles (*Emydoidea blandingii*): implications for conservation and management of long-lived organisms. Conservation Biology 7, 826–833.

Congdon, J.D., Dunham, A.E., Van Loben Sels, R.C., 1994. Demographics of common snapping turtles (*Chelydra serpentina*): implications for conservation and management of long-lived organisms. American Zoologist 34, 397–408.

Cox, J., 1989. Survival characteristics of small tortoise populations and their possible influence on relocation efforts. In: Diemer, J.E., Jackson, D.R., Landers, J.L., Layne, J.N., Wood, D.A. (Eds.), Gopher Tortoise Relocation Symposium Proceedings. Florida Game and Fresh Water Fish Commission Nongame Wildlife Technical Report #5, Tallahassee, Florida, pp. 7–14.

Dodd Jr., C.K., 1988. Disease and population declines in the flattened musk turtle *Sternotherus depressus*. American Midland Naturalist 119, 394–401.

Dodd Jr., C.K., Ozgul, A., Oli, M.K., 2006. The influence of past disturbance events on survival and dispersal rates of Florida box turtles. Ecological Applications 16, 1936–1944.

Doonan, T.J., 1986. A demographic study of an isolated population of the gopher tortoise, *Gopherus polyphemus*; and an assessment of a relocation procedure for tortoises. M.S. Thesis, University of Central Florida, Orlando, FL, 93 pp.

Dorcas, M.E., Willson, J.D., Gibbons, J.W., 2007. Crab trapping causes population decline and demographic changes in diamondback terrapins over two decades. Biological Conservation 137, 334–340.

Enge, K.M., Millsap, B.A., Doonan, T.J., Gore, J.A., Douglass, N.J., Sprandel, G.L., 2002. Conservation plans for biotic regions in Florida containing multiple rare or declining wildlife taxa. Florida Fish and Wildlife Conservation Commission Technical Report 20, Tallahassee, FL, USA.

Eubanks, J.O., Michener, W.K., Guyer, C., 2003. Patterns of movement and burrow use in a population of gopher tortoises (*Gopherus polyphemus*). Herpetologica 59, 311–321.

Field, K.J., Tracy, C.R., Medica, P.A., Marlow, R.W., Corn, P.S., 2007. Return to the wild: translocation as a tool in the conservation of the desert tortoise (*Gopherus agassizii*). Biological Conservation 136, 232–245.

Florida Fish and Wildlife Conservation Commission, 2002. Petition to List the Gopher Tortoise (*Gopherus polyphemus*) as a Threatened Species in Florida. Florida Fish and Wildlife Conservation Commission, Tallahassee, FL, USA.

Fonnesbeck, C.J., Dodd Jr., C.K., 2003. Estimation of flattened musk turtle (*Sternotherus depressus*) survival, recapture, and recovery rate during and after a disease outbreak. Journal of Herpetology 37, 602–607.

Fordham, D.A., Georges, A., Brook, B.W., 2007. Demographic response of snake-necked turtles correlates with indigenous harvest and feral pig predation in tropical northern Australia. Journal of Animal Ecology 76, 1231–1243.

Fordham, D.A., Georges, A., Brook, B.W., 2008. Indigenous harvest, exotic pig predation and local persistence of a long-lived vertebrate: managing a tropical freshwater turtle for sustainability and conservation. Journal of Applied Ecology 45, 52–62.

Frazer, N.B., 1992. Sea turtle conservation and half-way technology. Conservation Biology 6, 179–184.

Gates, C.A., Allen, M.J., Diemer Berish, J.E., Stillwaugh Jr., D.M., Shatter, S.R., 2002. Characterization of a gopher tortoise mortality event in west-central Florida. Florida Scientist 65, 185–197.

Germano, D.J., Joyner, M.A., 1988. Changes in a desert tortoise (*Gopherus agassizii*) population after a period of high mortality. Management of Amphibians, Reptiles, and Small Mammals in North America. US Department of the Interior, US Forest Service, Ft. Collins, Colorado. pp. 190–198.

Gibbs, J.P., Shriver, W.G., 2002. Estimating the effects of road mortality on turtle populations. Conservation Biology 16, 1647–1652.

Heise, C.D., Epperson, D.M., 2005. Site fidelity and home range of relocated gopher tortoises in Mississippi. Applied Herpetology 2, 171–186.

Heppell, S.S., 1998. Application of life-history theory and population model analysis to turtle conservation. Copeia 1998, 367–375.

Heppell, S.S., Crowder, L.B., Crouse, D.T., 1996. Models to evaluate headstarting as a management tool for long-lived turtles. Ecological Applications 6, 556–565.

Hoyle, M.E., Gibbons, J.W., 2000. Use of marked population of diamondback terrapins (*Malaclemys terrapin*) to determine impacts of recreational crab pots. Chelonian Conservation and Biology 3, 735–737.

Iverson, J.B., 1991. Patterns of survivorship in turtles (order Testudines). Canadian Journal of Zoology 69, 385–391.

Longshore, K.M., Jaeger, J.J., Sappington, J.M., 2003. Desert tortoise (*Gopherus agassizii*) survival at two eastern Mojave Desert sites: death by short-term drought? Journal of Herpetology 37, 169–177.

Moll, E.O., 1979. Reproductive cycles and adaptations. In: Harless, M., Morlock, H. (Eds.), Turtles: Perspectives and Research. John Wiley and Sons, New York, pp. 305–331.

Morafka, D.J., 1994. Neonates: missing links in the life histories of North American tortoises. In: Bury, R.B., Germano, D.J. (Eds.), Biology of North American Tortoises. US Fish and Wildlife Service, Wildlife Research Report, Washington, DC, pp. 161–173.

O'Brien, S., Robert, B., Tiandry, H., 2005. Consequences of violating the recapture duration assumption of mark-recapture models: a test using simulated and empirical data from an endangered tortoise population. Journal of Applied Ecology 42, 1096–1104.

Pedrono, M., Smith, L.L., Clobert, J., Massot, M., Sarrazin, F., 2004. Wild-captive metapopulation viability analysis. Biological Conservation 119, 463–473.

Reed, R.N., Congdon, J., Gibbons, J.W., 2005. The alligator snapping turtle [*Macrochelys* (*Macroclemys*) *temminckii*]: a review of ecology, life history, and conservation, with demographic analyses of the sustainability of take from wild populations. A report to Division of Scientific Authority, United States Fish and Wildlife Service, 17 pp.

Sarrazin, F., Barbault, R., 1996. Reintroduction: challenges and lessons for basic ecology. Trends in Ecology and Evolution 11, 474–478.

Seigel, R.A., Dodd, C.K., 2000. Manipulations of turtle populations for conservation: halfway technologies or viable options? In: Klemens, M.W. (Eds.), Turtle Conservation. Smithsonian Institution Press, Washington, DC, pp. 218–238.

Seigel, R.A., Smith, R.B., Seigel, N.A., 2003. Swine flu or 1918 pandemic? Upper Respiratory Tract Disease and the sudden mortality of gopher tortoises (*Gopherus polyphemus*) on a protected habitat in Florida. Journal of Herpetology 37, 137–144.

Stubbs, D., Swingland, I.R., Hailey, A., Pulford, E., 1985. The ecology of the Mediterranean tortoise *Testudo hermanni* in northern Greece (the effects of a catastrophe on population structure and density). Biological Conservation 31, 125–152.

Taylor, R.W., 1982. Human predation on the gopher tortoise (*Gopherus polyphemus*) in north-central Florida. Bulletin of the Florida State Museum. Biological Sciences 28, 79–102.

Thomas, D.H., Jones, G.D., Durham, R.S., Larsen, C.S., 1978. The anthropology of St. Catherines Island – 1. Natural and cultural history. Anthropological Papers of the American Museum of Natural History, vol. 55.

Tuberville, T.D., 2008. Evaluating the success of translocations for turtle conservation: a case study based on behavioral and demographic responses of the gopher tortoise, *Gopherus polyphemus*. Ph.D. Thesis. University of Georgia, Athens, Georgia, USA.

Tuberville, T.D., Clark, E.E., Buhlmann, K.A., Gibbons, J.W., 2005. Translocation as a conservation tool: site fidelity and movements of repatriated gopher tortoises (*Gopherus polyphemus*). Animal Conservation 8, 349–358.

US Fish and Wildlife Service, 1994. Desert tortoise (Mojave population) recovery plan. US Fish and Wildlife Service, Portland, OR.

White, G.C., Burnham, K.P., 1999. Program MARK: survival estimation from populations of marked animals. Bird Study (46 Suppl.), 120–138.

Wilbur, H.M., Morin, P.J., 1988. Life history evolution in turtles. In: Gans, C., Huey, R. (Eds.), . In: Biology of the Reptilia, vol. 16b. Alan R. Liss, Inc., New York, pp. 396–447.

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