Gopher tortoises (Gopherus polyphemus) once ranged throughout the southeastern United States (Auffenberg and Franz 1982). Today they are restricted to most of Florida, USA, and southern portions of 5 other states (Auffenberg and Franz 1982). They are listed as a species of special concern in the state of Florida (Enge et al. 2002) and federally or state-listed as threatened or endangered over the rest of their range (Gopher Tortoise Council 2000). Although human predation had a substantial effect on gopher tortoise populations prior to legal protection (Taylor 1982), habitat destruction is currently the main threat (Diemer 1986). In Florida, the human population grew 23.5% during the 1990s from 12.9 million to 16 million (United States Census Bureau 2003a). During that same time period, the number of housing units rose 20% from 6.1 million to 7.3 million (United States Census Bureau 2003b). Such tremendous growth leads to conflict with gopher tortoise populations. State-issued guidelines direct officials to exhaust all other conservation options before considering relocations as a last-resort solution to such conflicts (Florida Game and Fresh Water Fish Commission 1988). Despite this recommendation, relocations of gopher tortoises in Florida are common. In the 1990s alone, >25,000 gopher tortoises were permitted for relocation in Florida (Enge et al. 2002), and many more relocations are presumed to occur without permitting. Probably no other reptile has been so commonly relocated, both legally and illegally, for conservation purposes.

Though relocations of gopher tortoises are frequent, retention of relocated individuals has rarely been evaluated. Of the 10 follow-up studies that we found, 7 were conducted after ≤1 year, 2 were conducted after 2 years, and the longest was conducted after 5 years (Table 1). Recapture rates of relocated individuals varied from 17% to 100%, with values of 17% to 45% for studies of ≥1 year. These recapture rates have led to dire predictions for the fate of relocated gopher tortoise populations. For instance, Seigel and Dodd (2000) conducted a population viability analysis (PVA) for a theoretical relocated population of gopher tortoises. In their PVA they began with 50 adults, used empirical data on reproduction and hatchling survival, and assumed constant adult survival rates (considered equivalent to retention) of 80%, 85%, 90%, and 95% to evaluate the impact of retention on viability. Within 30 years, populations with adult retention rates of 80% were extinct, and those with retention rates of 85% were nearing extinction. A critical assumption by Seigel and Dodd (2000) is that retention rates are constant over time. If this assumption is true, and retention rates observed over short time periods (e.g., 17–45% over 2–5 yr; Table 1) are sustained long term, relocations cannot lead to establishment of viable populations. These results suggest that relocations are of little value, and perhaps should not be permitted at all. However, the key assumption of the Seigel and Dodd (2000) model, that retention rates are constant over long periods of time, is untested.

Our study followed up on the relocation reported by Burke (1989). For ease of analysis, here we focus only on the 74 tortoises involved in the original relocation in 1985. A...
follow-up survey in 1986 found 31 of the 74 gopher tortoises that had been relocated a year earlier. In 1987, 2 years after relocation, 33 of the gopher tortoises were found. Thus, the retention rate 1 year after relocation was 42% but over 100% from year 1 to year 2 (2 individuals were captured in 1987 but not in 1986), suggesting that retention rates are low during the first year postrelocation but high thereafter. Our objectives were to examine individual and population-level retention, growth, and reproduction of this relocated population of gopher tortoises 17 years after relocation, measure growth rates and prevalence of upper respiratory tract disease (URTDM), a disease associated with population declines for this and other tortoise species (Diemer Berish et al. 2000, Brown et al. 2002, Gates et al. 2002), and evaluate the health of the relocated population. Our final objective was to evaluate long-term viability prospects for this population.

### STUDY AREA

Our study (Table 1) followed up on a 1985 relocation in which gopher tortoises were moved from a development site (Regional Development Center) in Palm Beach County, Florida (Burke 1989). In 1985, cabbage palm (Sabal palmetto) flatwoods were the dominant vegetation association at both sites. Gopher tortoises had been present historically at OCP; however, they had been extirpated by humans prior to the 1985 relocation (Burke 1989). No site management had been done to specifically prepare OCP for the relocation, but OCP had burned in 1980.

In 2002 as in 1985, Okeeheelee County Park consisted of 28.6 ha of suitable habitat at the nature area of OCP for gopher tortoises and their burrows. We conducted surveys at this time (Jun–Aug) to maximize capture of individuals because, in this region, gopher tortoises are most active from May through September (Douglass and Layne 1978). To survey the site, we performed line transects with 4–10 surveyors spaced 5 m apart. This spacing was close enough to see the entire ground area between surveyors, even in dense vegetation. To ensure that surveyors did not miss burrows, 1–2 researchers walked behind the surveyors. We did not survey other portions of OCP because our study was directed toward evaluating retention at the relocation site.

We captured gopher tortoises primarily at burrows. We first attempted to lure tortoises out of each potentially occupied burrow (we ignored only burrows that did not have well-defined openings) by slapping the ground at the mouth of the burrow and then hand-bobbing (Burke and Cox 1988). Most gopher tortoises responded by approaching. Once the tortoise was near, we gained hold of it and pulled it from the burrow, taking care not to damage the burrow. Some tortoises, particularly smaller individuals, responded to our hand-bobbing by retreating further into the burrow. In these cases we placed a bucket trap at the burrow entrance. A bucket trap consisted of an 18.9-L bucket sunk into the ground at the burrow opening, covered with brown paper. We checked buckets 2–3 times per day until we captured the tortoise. We captured some gopher tortoises while they were active above ground.

Upon capture we checked marginal scutes of each tortoise for previous drill marks. If drill marks were present, we matched them to combinations of drill marks given to individuals prior to relocation in 1985. If a tortoise did not have any drill marks, we gave it a cohort drill mark (we drilled a hole in the same marginal scute for all new individuals captured in 2002) and injected a PIT-tag (model TX1400L, 125 kHz, 11.5 x 2 mm, 0.06 g; Biomark, Inc., Meridian, ID) into the inguinal area of each tortoise to permit future identification. We used concavity of the plastron, a secondary sexual characteristic, to infer gender of each adult individual (McRae et al. 1981); we did not identify gender of juveniles. We measured straight-line carapace length (CL; ±1 mm) using tree-calipers. We checked each tortoise for external symptoms of infection of Mycoplasma agassizii, the bacterium that causes upper respiratory tract disease (Brown et al. 1999). Symptoms include nasal discharge, ocular discharge, conjunctivitis, and swollen eyelids (Brown et al. 1999).

<table>
<thead>
<tr>
<th>N₀</th>
<th>Time</th>
<th>N₁</th>
<th>(N₁/N₀) × 100 (%)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>40</td>
<td>3</td>
<td>18</td>
<td>45</td>
<td>Lohofeneer and Lohmeier 1986</td>
</tr>
<tr>
<td>98</td>
<td>6</td>
<td>78</td>
<td>80</td>
<td>Dietlein and Smith 1979</td>
</tr>
<tr>
<td>25</td>
<td>6</td>
<td>25</td>
<td>100</td>
<td>Stout et al. 1989</td>
</tr>
<tr>
<td>10</td>
<td>10</td>
<td>2</td>
<td>20</td>
<td>Dietlein and Smith 1979</td>
</tr>
<tr>
<td>10</td>
<td>10</td>
<td>5</td>
<td>50</td>
<td>Stout et al. 1989</td>
</tr>
<tr>
<td>17</td>
<td>11</td>
<td>15</td>
<td>88</td>
<td>Fucigna and Nickerson 1989</td>
</tr>
<tr>
<td>12</td>
<td>12</td>
<td>7</td>
<td>58</td>
<td>Stout et al. 1989</td>
</tr>
<tr>
<td>144</td>
<td>22–24</td>
<td>25</td>
<td>17</td>
<td>Godley 1989</td>
</tr>
<tr>
<td>74</td>
<td>24</td>
<td>33</td>
<td>45</td>
<td>Burke 1989</td>
</tr>
<tr>
<td>24</td>
<td>60</td>
<td>7</td>
<td>29</td>
<td>Diemer 1987</td>
</tr>
</tbody>
</table>

Table 1. Retention of relocated populations of gopher tortoises in the southeastern United States prior to 2002. N₀ = number of tortoises released. Time = duration (months) between release and follow-up survey. N₁ = number of tortoises captured at follow-up census that were released in original relocation. (N₁/N₀) × 100 = percentage of relocated tortoises retained on-site. Arranged by time between release and follow-up census.
When compiling retention rates for this study, we re-examined the data collected by Burke (1987, 1989). We found that although percentages of retained individuals were similar 1 year and 2 years postrelocation (42% and 45%, respectively), the same individuals were not captured in each survey. This was also true for 2002 surveys (i.e., some relocated individuals captured in 2002 were not detected in surveys in 1986, 1987, or neither). Therefore, when evaluating changes in retention rates over time we used 2 approaches. First, we used the percentage of relocated individuals captured at each postrelocation survey. Second, we assumed that all individuals present in a later survey had in fact been present in earlier surveys. In other words, if a tortoise was detected in the 1986 and 2002 surveys but not in the 1987 survey, we assumed that it had been present for all 3 surveys but was missed in the 1987 survey.

Berry (1986) hypothesized that retention rates would be higher for relocated juveniles than for relocated adults and higher for relocated adult females than for relocated adult males. Therefore, we used chi-square analyses of our data to test the hypotheses that retention rates are greater for juveniles than adults and for adult females than adult males.

RESULTS

In 2002, we captured 31 gopher tortoises with drill marks matching records for individuals relocated in 1985. Thus, percentage of the original gopher tortoise population retained on-site was 42% after 1 year, 45% after 2 years, and 42% after 17 years (Fig. 1a).

However, only 11 individuals were captured in all 3 (1986, 1987, and 2002) surveys. Therefore, most relocated individuals captured in 2002 were missed in either or both of the earlier surveys. We also plotted retention rates over time based on the assumption that any tortoise present in a later survey had been present but missed in earlier surveys. With these data, we estimate that 54 of 74 individuals were present 1 year postrelocation, 48 of 74 tortoises were present 2 years postrelocation, and 31 of 74 individuals were present 17 years later (Fig. 1b). This shows a 27% decline in number of relocated individuals on-site during the first year (73% retention), 8% during the second year (92% retention), and a mean of 1.5% over the subsequent 15 years (98.5% retention).

In 2002, we captured 13 of 28 adult males, 8 of 23 adult females, and 10 of 23 juveniles released in 1985. Percentages of individuals recaptured 17 years later did not differ significantly between juveniles and adults (43% and 41%, respectively; \( \chi^2 = 0.05, \text{df} = 1, P = 0.83 \)). Percentages of individuals released as adult males and adult females that we recaptured 17 years later did not differ significantly (46% and 35%, respectively; \( \chi^2 = 1.49, \text{df} = 1, P = 0.22 \)).

When calculated over 17 years (from release in 1985 to follow-up in 2002), carapace length growth rate for 10 individuals originally released as juveniles ranged from 5.1 mm CL/year to 10.8 mm CL/year, with a mean of 7.6 ± 1.9 mm CL/year. All individuals released as juveniles in 1985 were adults in 2002. Growth rates between initial release in 1985 and recapture in 2002 for 8 individuals released as adult females averaged 1.8 ± 1.9 mm CL/year, ranging from 0 mm CL/year to 5.3 mm CL/year. Over the same time period, growth rates for 12 individuals originally released as adult males averaged 1.6 ± 1.4 mm CL/year, ranging from 0.1 mm CL/year to 4.5 mm CL/year.

With respect to URTD symptoms, 16% of individuals (5 of 31) showed nasal symptoms, 13% (4 of 31) ocular symptoms, 10% (3 of 31) conjunctivitis, and 19% (6 of 31) palpebral edema. Overall, 35% (11 of 31) of individuals had \( \geq \)1 URTD symptom. Of individuals showing \( \geq \)1 clinical sign of URTD, 7 were males and 4 were females.

DISCUSSION

Successful relocations require individual retention, growth, and reproduction, as well as indications that these characteristics will persist (e.g., maintenance of high habitat quality and large population size; Griffith et al. 1989, Wolf et al.
Our study is the first to measure retention rates of relocated populations of gopher tortoises over long periods of time, a critical component of PVAs of relocated populations. For example, Seigel and Dodd's (2000) PVA assumed constant retention rates and found that tortoise populations with retention rates ≤85% were at or near extinction within 30 years. We found that retention during the first year was 42%, but retention was 100% during year 2 through year 17 when we used only the percentage of relocated individuals captured at each postrelocation survey. However, we consider the estimated retention rates based on the assumption that individuals in later surveys were undetected in earlier surveys to be better indicators of actual retention rates. Using these estimates, we found a retention rate of 73% during the first year postrelocation, 92% during the second year postrelocation, and 98.5% on average from year 2 through year 17. In other words, retention rates were low during the first year after relocation but then high (92–100%) each year up to year 17. These data are biased low because our 2002 surveys had detection probabilities <1.0. Our data suggest that retention rates can be high, and that they change over time, a phenomenon that should be considered when conducting population viability analyses of relocated populations.

It has been suggested that retention of tortoises may be affected by the gender and age of the relocated individuals. For example, Berry (1986) hypothesized that relocations should rely primarily on juveniles because they are more likely to be retained due to minimal disruption of existing social structures and, of adults, females are more likely to be retained due to their smaller home ranges and less cohesive social structures. Consistent with Burke (1989), we did not find support for either of these hypotheses. Adults were just as likely to be retained as juveniles, and adult males were actually more likely to be retained than adult females (though the difference was not significant). One reason that age and sex may not have had an effect on retention rates of our relocated population is that no tortoises were present on-site prior to the 1985 relocations. To further evaluate these hypotheses, we recommend studies of retention of individuals that have been relocated into areas with resident tortoises.

In addition to retention, we sought evidence of normal growth and reproduction of relocated tortoises. We found that relocated gopher tortoises grew at rates similar to other populations (e.g., Landers et al. 1982, Mushinsky et al. 1994, Aresco and Guyer 1999), indicating generally good health. However, we are concerned about the long-term viability of this population because of a possible lack of recruitment, despite unambiguous evidence of reproduction. We only found 2 large juveniles (180 mm and 190 mm CL) at OCP in 2002, whereas juveniles composed approximately 30% of the population at relocation in 1985 (Burke 1989). Thus, we did not detect juveniles, particularly very young gopher tortoises, at OCP in 2002. As further evidence for the dearth of juveniles, the smallest burrows at OCP in 2002 measured 180 mm wide at 20-cm depth (following Martin and Layne 1987). Burrow width is strongly correlated with CL for gopher tortoises (Martin and Layne 1987); not only did the smallest individuals captured at OCP in 2002 measure 180 mm CL and 190 mm CL, but the smallest burrows found on-site corresponded to these body sizes.

One could argue that our search method was unlikely to find juveniles and their burrows, but that is not the case. First, one of us (R. L. Burke) located juvenile burrows on the same site in 1986 and 1987. Second, identical surveys of other Florida gopher tortoise populations conducted by one of us (K. G. Ashton) yielded a total of 368 active and inactive burrows (indicating current or recent activity; Auffenberg and Franz 1982), ranging in size from 40 mm to 560 mm wide (at 20-cm depth), with 20% of all burrows measuring <180 mm wide (the smallest burrow detected at OCP). Therefore, although relocated gopher tortoises remain at OCP 17 years postrelocation, the long-term viability of this population is questionable due to a lack of recruitment.

Another concern for this population is the finding that 11 of the 31 relocated individuals showed ≥1 symptom of URTD, with 7 individuals having severe (ocular or nasal mucous discharge) symptoms. Declines in both relocated and non-relocated tortoise populations have been associated with URTD prevalence (Diemer Berish et al. 2000, Brown et al. 2002, Gates et al. 2002).

**MANAGEMENT IMPLICATIONS**

Although our study demonstrates that relocation can result in long-term on-site retention of gopher tortoises, we agree with Burke (1991), Seigel and Dodd (2000), and others (Florida Game and Fresh Water Fish Commission 1988) that relocations are an intensive manipulation and should only be considered after a careful examination of other options, as well as the costs, logistical difficulties, and probability of success of relocations. When relocations are performed, we advise conservation planners do the following: 1) relocate a large number of individuals (≥100 individuals, if possible); 2) relocate individuals to an area with high habitat quality within their native range; and 3) maintain high habitat quality after relocation.

**ACKNOWLEDGMENTS**

We thank the staff and volunteers at Okeechobee County Park for access and assistance, particularly C. Pinnock, D. Campbell, and C. Manyi; A. Knipps and volunteers from the Earthwatch Institute for field assistance; D. Voss and staff at Greenacres Veterinary Clinic for X rays; R. Pickert for Global Positioning System and Geographic Information System assistance; Florida Fish and Wildlife Conservation Commission for permit (no. WX02130); and Archbold Biological Station and Earthwatch Institute for support.

**LITERATURE CITED**


Auffenberg, W., and R. Franz. 1982. The status and distribution of the


Florida Game and Fresh Water Fish Commission. 1998. Guidelines for gopher tortoise relocations. Florida Game and Fresh Water Fish Commission, Tallahassee, USA.


Associate Editor: Lanham.