# Dispersal, home range establishment, survival, and reproduction of translocated eastern box turtles, *Terrapene c. carolina*

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**Abstract.** The feasibility of translocation to establish a population of the eastern box turtle (*Terrapene c. carolina*) was studied at Floyd Bennett Field, Brooklyn, New York, USA. The 579 ha site, originally salt marsh, was filled during the 1920's to construct a now-abandoned airport. It consists primarily of grasslands, native shrub thickets and woodlands, and mixed stands dominated by giant reed (*Phragmites australis*). These human-created uplands are managed by the U.S. National Park Service for recreation and ecological restoration. Prior to this work, the site did not support a population of this species, but it is historically native to adjacent uplands. *T. c. carolina* were collected from sites on Long Island, New York, that were undergoing development, and released after data on size, mass, age, and sex were recorded. From 1987 through 1990, 335 individuals were released into developing woodlands. To provide data on dispersal, home range establishment, and initial survival, fifty-three of these were radio-tracked for up to seven years. Though individually variable, the *T. carolina* dispersed homeward. Of the 53 radio-tagged individuals, 13 (24.6%) left the site, 25 (47.2%) established home ranges, and 15 (28.3%) died before determination of home range establishment could be made. Most individuals established home ranges within a kilometer of the release point. However, some dispersed greater distances. Of the 25 individuals that established home ranges, 17 (68%) did so in the release year, two (8%) in outyear 1, three (12%) in outyear 2, and three (12%) in outyear 3. Annual known survival over five years post-release was 71%. Though not statistically significant, annual survival was 64% over the first two years and 84% over the final three. Principal causes of "mortality" were dispersal from the site and pneumonia, both of which were greatest initially, plus winter kill, a random event. Patterns of growth, home range size, activity season, habitat use, annual reproductive output, and production of young were generally comparable to natural populations of *T. carolina.* These results suggest that translocation may have potential for establishing new populations of *T. carolina*, though long term viability is still uncertain. However, any contemplated translocation would need to address the initially high loss to dispersal and disease. Moreover, since there are few sites of adequate size and quality, at least 500 ha of predominantly woody habitat, lacking populations of this species, its appropriateness is very limited.

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*Key words*: Dispersal; home range; homing; mortality; persistence; reproduction; survival; *Terrapene carolina*; translocation.

## Introduction

Chelonian decline is a global issue that in recent decades appears to have increased in scope and severity (Behler, 1997; Gibbons et al., 2000; Klemens, 1997). Causes are many and complex, as are solutions (Klemens, 2000). Among the techniques to address this issue are Repatriation, Relocation, and Translocation (RRT). While definitions vary between authors (Griffith et al., 1989; Reinert, 1991; Dodd and Seigel, 1991; Dodd, 2001), all essentially involve taking individuals of a species from one place and releasing them at another, either to establish a new population, augment an existing one, or remove animals from harm's way.

Though popular with government agencies and the public, many conservation professionals question the effectiveness of RRT programs, particularly at establishing viable populations. RRT programs may only be a politically expedient remedy of dubious value, creating an illusion of effectiveness while undermining effective but more difficult to enact conservation strategies based on habitat protection (Dodd and Seigel, 1991; Seigel and Dodd, 2000; McDougal, 2000).

Though instances can be found for many species of chelonians, RRT programs for gopher tortoise (*Gopherus polyphemus*) and desert tortoise (*G. agassizii*) have been the most extensively studied. Collectively, studies of gopher tortoise RRT programs have provided minimal or conflicting data regarding the fate of relocated animals (Diemer, 1989). In a similar review of desert tortoise RRT programs, Berry (1986) noted that tortoises may die, become established at release sites, disperse in various directions, or attempt to return home. Existing data were insufficient to determine the frequencies of these responses.

Formal RRT programs involving *Terrapene* are few. *Terrapene*, especially *T. carolina*, have previously been considered common (Ernst and Barbour, 1972) and thus a low conservation priority. In recent years this has changed (Dodd, 2001). *T. ornata* is now listed as endangered or threatened in a number of American states, and *T. carolina* is listed as a species of special concern by some states in the northeast United States. Population declines in *T. carolina* have been reported in New England (DeGraaf and Rudis, 1983), Michigan (Harding, 1995), Indiana (Williams and Parker, 1987), Maryland (Hall et al., 1999), Alabama (Mount, 1986), and Florida (Dodd and Franz, 1993). Urbanization, agriculture, logging and road construction, coupled with commercial over-collecting, pose a serious threat to long term viability of *Terrapene* populations (Lieberman, 1994). In the New York City area, where this work took place, *T. c. carolina* has been extirpated within city limits and has declined in adjacent suburban counties, though populations still survive in patchwork habitats (Klemens, 1989; Schlauch, 1978).

With growing concern over *Terrapene* populations, RRT programs are being looked to as a management tool, particularly for salvaging individuals from remnant populations being lost to development (Doroff and Keith, 1990; Belzer, 1999; Hatch et al., 2000). In addition, throughout its range, numerous *T. carolina* found crossing roads or otherwise at risk are often moved by concerned citizens to sites (generally with extant populations) deemed safe from development and other threats (e.g. Anonymous, 1993).

As with *Gopherus*, translocated *Terrapene* exhibit a range of responses. Homing in *Terrapene* is well documented (Lemkau, 1970; Madden, 1975; Nichols, 1939), and translocated individuals may not remain on the release site. However, there are many cases where individuals, particularly those moved in excess of 5-10 km, remained at the release site or did not home (Doroff and Keith, 1990; Gould, 1957, 1959; Nichols, 1939; Posey, 1979; Schwartz and Schwartz, 1974). In addition, while movements may not be homeward, they may still be orientated, and result in individuals leaving the release site (Hall, 1987). Though these studies document the different post-release responses, because of limitations in methodology, duration, sample size, or distance moved, they provide little data on the frequency of these responses.

As part of a program of herpetofaunal community restoration/re-creation (Cook, 2002; Cook and Pinnock, 1987), eastern box turtles (*T. c. carolina*) were released at Floyd Bennett Field, Brooklyn, New York, USA. While the ultimate goal was to establish a population on this now-protected, but faunally depauperate habitat island, a second and more immediate one was to document post-release movement and ecology of translocated *T. c. carolina*.

## Methods

### *Release site*

Floyd Bennett Field (FBF) is a peninsula projecting southward into Jamaica Bay, Long Island, New York. It is bounded basally by a highway and dense urbanization, making it a habitat island. Originally salt marsh, the uplands of this 579 ha site were created by dredge spoil deposition from ca. 1928 through 1945. Despite its history, FBF is a significant habitat for wildlife in this heavily urbanized region, and is managed for recreation and ecological restoration by the U.S. National Park Service as part of Gateway National Recreation Area (fig. 1). Since FBF's uplands are human created, this program is a translocation (Dodd, 2001). However, *T. c. carolina* were historically native to the adjacent (now urbanized) uplands, and habitats on FBF contain many elements of the area's native vegetation.

Though ecologically young, succession was increasing native woody plant dominance. The site consisted of early successional habitats; mixed grasslands; shrub thickets dominated by bayberry (*Myrica pennsylvanica*), blackberry (*Rubus* sp.), and sumacs (*Rhus* sp.); pioneering woodlands of black cherry (*Prunus serotina*),

**Figure 1.** Location of Floyd Bennett Field, Brooklyn, NY.

grey birch (*Betula populifolia*), aspen and cottonwood (*Populus* sp.), and mulberry (*Morus rubra*); freshwater marshes dominated by sedges (*Carex* sp.) and ferns; a 0.3 ha freshwater pond created in 1989; and stands dominated by giant reed (*Phragmites australis*) (Cook and Tanacredi, 1990). The relatively large vegetated tracts are separated by paved runways ranging from 33 to 100 m wide.

### *Translocation and post-release monitoring*

From 1987 through 1990, 335 eastern box turtles were collected in Nassau and Suffolk Counties, Long Island, New York, and released at FBF, under a Scientific Collection License from the New York State Department of Environmental Conservation. Individuals were collected from sites being developed or while crossing roads in fragmented, suburban neighborhoods. All were marked by shell notching (Cagle, 1939) and with numbered Peterson disc tags, and data on size, mass, age category (1 = juvenile, 2 = young adult, 3 = middle aged adult, 4 = old adult (Cook, 1996)), sex, and reproductive condition recorded. To study dispersal, home range establishment, and survival, 53 individuals were randomly selected and released with radio-tags mounted with epoxy resin to the turtle's carapace (Larson, 1984).

Histories of the translocated *Terrapene* differed. Some were collected just prior to translocation, while others had been held as pets for varying periods of time. The extent to which different histories might affect post-release movement was unknown, but considered potentially significant. In addition, since accounts of *T. carolina* returning to holding pens after release (Gould, 1957) suggest acclimation, and pens had been used with varied results in gopher tortoise RRT programs (Godley, 1989; Stout et al., 1989), it was thought that holding animals in pens at the release site might lessen potential homing response. This was tested by holding animals in a pen for either 0 or 15 days (Burke, 1989).

Box turtles released with radio transmitters were divided into four categories ("Wild 0", "Wild 15", "Pet 0", "Pet 15") reflecting differences in handling prior to arriving, and at the release site. Each category had 12 to 15 individuals. "Wild" individuals were collected and brought to the release point within seven days. "Pets" were individuals held in captivity, off-site, for a minimum of thirty days. Turtles were randomly selected to be either released immediately (0 days) or held in an acclimation pen at the release point for 15 days prior to release. The remaining 282 individuals were held in the acclimation pen for 30 days and released without radio transmitters.

Radio-tagged turtles were recaptured using an AVM LA-12 radio receiver and data on location, weather, habitat, heading, mass, and behavior recorded. Location was recorded as distance (measured by range finder) and compass bearing from a series of marked reference points, discernible both in the field and on 1 : 2400 aerial photographs. Locations were plotted on aerial photographs and converted to UTM coordinates using a digitizing table.

Generally, turtles were recaptured daily the first three days following release, then weekly and, as time elapsed, less frequently. Individuals showing rapid or "unusual" movements were monitored more intensely than slower or sedentary individuals. Intensity of long term monitoring varied, with recapture intervals ranging from one to three weeks. Due to transmitter failure early in the study, there is considerable variation between individuals in the duration and intensity of monitoring data.

In 1992 and 1993, radios were placed on 20 additional turtles. They had originally been released without radios, and by 1992-1993 had established home ranges. In 1992 and 1993 all radio-tagged animals were monitored weekly. All transmitters were removed on 15 December 1993, though some active search continued through 1995. Throughout the study, recaptures of animals without radios or with non-functional radios were made incidental to radio-tracking or in active search. From 1993 through 1995 a trained Labrador retriever was used to find and retrieve turtles (Schwartz and Schwartz, 1974).

Fecundity was estimated by palpating females for eggs whenever possible or by X-raying (Gibbons and Greene, 1979). Since an accurate determination of fecundity rate requires X-raying females in a population on a number of occasions during the egg-laying season, only 1993 data are reasonably comprehensive. Clutch size data were obtained from X-rays of gravid females and from the nest of T505 in 1995. Progeny (i.e. unmarked young) were recorded whenever encountered.

Data from the 53 individuals released with radios were used to analyze dispersal direction, speed, and distance, survival, and home range establishment. Data from these 53, plus the 20 additional individuals radio-tagged in 1992-1993, were used to estimate home range size and stability, and reproductive output.

### *Analysis of dispersal and home range*

Analysis of dispersal direction was based on "vanishing bearings", the direction from release point that an animal disperses. Madden (1975) found that some displaced *Terrapene* wandered randomly for several days within 50 m of the release point before showing homeward movement. To separate initial random wanderings from potentially more orientated post-release movements, vanishing bearings were calculated as the bearing from release point to the point where the box turtles crossed imaginary circles 100 m and 200 m in radius, and centered on the release point. Since there were no differences between 100 m and 200 m vanishing bearings (Mardi-Watson-Wheeler test, $\chi^2 = 0.5$, df $= 2$, $p > 0.61$), analysis of dispersal direction was based on 200 m vanishing bearings. All bearings used were relative to magnetic north.

Randomness of dispersal was tested with the Rayleigh test (using actual vanishing bearings) and the V test, which incorporates knowledge of an expected dispersal direction, such as home. For the V test, home is set to 0° and actual vanishing bearings are transformed by making them relative to home. Homing was tested for by determining if the 95% confidence interval of the mean vanishing bearing included the population's home bearing (Batschelet, 1981). The Rayleigh and V tests apply to a population and can not determine if an individual homes. Similar to orientation studies of Gibbons and Smith (1968), individuals were considered to have homed if their vanishing bearing was within 45° of their home bearing.

Speed of initial dispersal (active season time taken to reach the 100 m radius, referred to as "time100") was evaluated using proportional hazards regression. In this use, "time100" was the "event time" of interest, and animals not recorded as crossing the 100 m radius due to death or radio malfunction were "censored" observations.

Locality data were used to calculate straight line distance from release point against time since release. Maximum recorded distance from release point, and the active season time taken to reach it were determined for individuals released with a radio. An activity season was 185 days, the number of days between mean dates of spring emergence and hibernation at FBF (Cook, 1996).

The 53 individuals released with radio tags were classified as having; 1) left the release site, 2) established a home range, or 3) died before the occurrence of one of these two events could be ascertained. Individuals that established home ranges showed a shift from uni-directional dispersal from the release point to a pattern of short distance, multi-directional movements within a relatively well-defined area (Cook, 1996). Since it was difficult to determine exactly when a home range is established, the year in which an animal's movements met these criteria was used to estimate the time to home range establishment.

Home range (Burt, 1943) was estimated for all radio-tagged individuals having a minimum of ten locations recorded subsequent to the year of home range establishment. These included individuals released with radios that established home ranges, plus the 20 additional individuals fitted with radios in 1992 and 1993. Home range size was calculated as the bivariate normal (95% ellipse) home range (Jennrich and Turner, 1969) using HOMERANGE (Ackerman et al., 1990) and the 95% harmonic means home range (Dixon and Chapman, 1980) using RANGES IV (Kenward, 1990). Bivariate normal home range allowed comparison with previous studies, whereas harmonic means estimates are sensitive to heterogeneity of habitat (Dixon and Chapman, 1980), and were considered more appropriate given FBF's patchiness. Due to heterogeneity of variance, analysis of home range size used log transformed (base 10) data. Differences in home range size due to age and sex were tested by two way ANOVA, all other factors were analyzed with one way ANOVA.

Stability of home ranges between years was evaluated by multivariate analysis of variance (MANOVA), testing for changes in home range geographic centers (mean $x$ and $y$ coordinates) (White and Garrot, 1990). Tests were performed between years with a minimum of 10 data points/year and a minimum of two months overlap in coverage between years (Madden, 1975). Stability of consecutive year's hibernacula was analyzed based on distance between hibernacula used in consecutive years by individuals that had established home ranges. Only hibernacula used after home range establishment were used.

### *Analysis of survival, mortality and persistence*

Assessment of survival was based on numbers of radio-tagged animals known to be alive, dead, or fate unknown. Individuals of unknown fate may have left the site, or may still be present, dead or alive. Since FBF is a habitat island surrounded by urbanization, individuals leaving the site are not likely to return or survive in the adjoining landscape. From a translocation perspective, animals leaving a release site represent mortality (Seigel and Dodd, 2000). Of the 14 animals whose fate was unknown at the end of this study, nine were lost track of in the release year and have been missing for three to five years (mean 4.6). Four were lost in the year after release, and have been missing two to four years (mean 3.5). Data on animals released without radios show that individuals not encountered (alive or dead) within three years of release were unlikely to be encountered over the longer term (Cook, 1996). Thus most, but not all, animals classified as fate unknown have likely left the release site. Known survival is a conservative estimate of known "persistence".

Since winter kill is a major mortality factor in *Terrapene* (Metcalf and Metcalf, 1979; Schwartz and Schwartz, 1974), estimates of annual survival are based on survival through the winter from one year to the next. Annual survival rates and 95% confidence limits were calculated using the "Known Fates" routine of program MARK (White and Burnham, 1999) based on animals known to be alive in a given year. This provides estimates comparable with *Terrapene* survival data from Stickel (1978), Schwartz and Schwartz (1991), and Williams and Parker (1987).

The relationship of survival to age, sex, origin ("pet" or "wild"), and time in holding pen (0 or 15 days) was analyzed two ways. Chi-square analysis compared known survival to three years and five years after release. Proportional hazards regression utilized time (in activity days) to death or disappearance, with animals alive at the conclusion of field work "censored" observations.

## Results

### *Dispersal and home range*

The mean bearing (mb) from release point to home (point of collection) for all turtles was 82.1° magnetic (vector length $r = 0.982$). Differences between the four treatment groups were not significant (Mardia-Watson-Wheeler test, $\chi^2 = 9.2$, df $= 6$, $p = 0.16$), reflecting the fact that all turtles were collected from east of the release site. Mean distance translocated was 70.2 km (SD $= 22.9$) and ranged from 32.2 to 131.3 km. Mean distance translocated by groups were; "pet0", 71.2 km; "pet15", 86.4 km; "wild0", 60.0 km; and "wild15", 66.9 km. There were significant differences between groups in distance translocated (one way ANOVA, $F_{3,48} = 3.32$, $p = 0.03$).

There were no significant between-group differences in actual vanishing bearings (Mardi-Watson-Wheeler test, $\chi^2 = 8.7$, df $= 6$, $p = 0.193$), and all individuals were pooled as a single population. The mean actual vanishing bearing, 66.0° ($r = 0.244$, $n = 52$) was significantly different from random (Rayleigh test, $z = 3.09$, $p = 0.05$). Between-group differences in transformed vanishing bearings were also not significant (Mardi-Watson-Wheeler test, $\chi^2 = 11.4$, df $= 6$, $p = 0.078$) and all individuals were again pooled. The mean transformed vanishing bearing, 336.0° ($r = 0.234$, $n = 52$; fig. 2) was significantly different from random (V test, $U = 2.18$, $p = 0.02$). The 95% confidence interval for the mean 200 m transformed vanishing bearing ranged from 280° to 32°, and included home (0°).

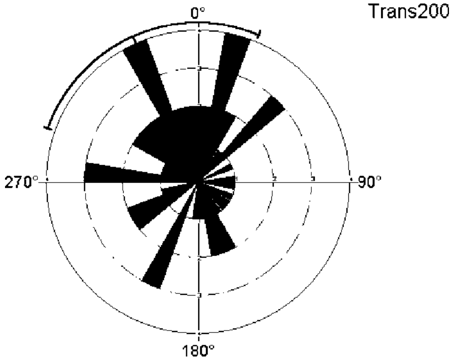

**Figure 2.** Transformed 200 m vanishing bearings of *T. carolina* translocated to Floyd Bennett Field, NY, showing distribution of individual bearings, mean and 95% confidence interval. Since home (0°) is within 95% confidence interval, homing can not be rejected.

There were no significant differences in vanishing bearings between individuals that established home ranges versus those that left the site (Mardia-Watson-Wheeler test, $\chi^2 = 2.7$, df $= 2$, $p > 0.1$). However, individuals that established home ranges were significantly oriented (mb $= 358°$, $r = 0.457$, hc $= 0.457$, $u = 3.231$, $p < 0.001$) and the 95% confidence interval for the mean bearing included the home bearing. In contrast, individuals that left the site were not significantly orientated (mb $= 300.5°$, $r = 0.280$, hc $= 0.142$, $u = 0.724$, $p > 0.10$) and did not home. Based on the index of homing performance, 46% of individuals (24/52) dispersed in a homeward direction (i.e. within 45° of homeward).

Time100 ranged from 0.3 to 460.0 days, with 75% of turtles reaching the 100 m radius in less than 54 days. Treatment group means ranged from 24.4 to 85.4 days, and overall mean time100 was 73.6 days. There were no significant differences in initial dispersal speed among the four treatment groups, nor due to origin ("pet" *vs* "wild"), holding in a pen, sex, or age. Initial dispersal speed of individuals that left the release site was significantly greater than those that established home ranges, and individuals that orientated homeward had significantly slower dispersal speed than those that did not (table 1). Speed of initial dispersal was weakly related to overall distance dispersed ($r = 0.28$, $p = 0.04$), indicating that initially fast moving individuals tended to disperse further than slow moving ones.

Straight-line distance from release point initially increased with time. In many cases, it eventually reached a maximum around which it generally fluctuated (figs 3, 4). However, there was considerable variation in this relationship and a number of general patterns emerge. Some individuals dispersed relatively fast and far, then settled, e.g. T323 (fig. 3), T365 (fig. 4). Others dispersed rapidly, and left the site. Turtle 512 reached a point 1020 m from the release point after 84 activity days and disappeared at the water's edge (fig. 4). Some individuals dispersed relatively far from the release point but took a few activity years to reach their maximum distance. For example T356 (fig. 3) ultimately attained a straight-line distance from release in excess of 800 m, but did not reach this distance until after

**Table 1.** Speed of initial dispersal in translocated *T. carolina*. Mean and quartile values (in activity days) of time to reach the 100 m radius (time100), and relationship to sex, age, pre-release treatment, and post-release fate. Q1, Q2, Q3, are 25%, 50%, and 75% quartile, respectively. Bold indicates statistical significance.

| Group | *n* | Time100 | | | | | Likelihood ratio test | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Mean | Q1 | Q2 | Q3 | SE | $\chi^2$ | df | *p* |
| All Inds | 52 | 73.56 | 5 | 29 | 54 | 18.44 | | | |
| Pet 0 | 14 | 85.41 | 4 | 30 | 55 | 39.50 | | | |
| Pet 15 | 11 | 72.64 | 6 | 32 | 54 | 40.11 | | | |
| Wild 0 | 15 | 24.35 | 5 | 9 | 47 | 7.10 | | | |
| Wild 15 | 12 | 59.29 | 13.5 | 33.5 | 104 | 18.96 | 1.1095 | 3 | 0.7748 |
| All pets | 25 | 80.93 | 6 | 32 | 55 | 28.84 | | | |
| All wild | 27 | 46.80 | 5 | 21 | 54 | 11.79 | 0.8146 | 1 | 0.3668 |
| Held 0 day | 29 | 71.95 | 5 | 21 | 55 | 25.45 | | | |
| Held 15 day | 23 | 69.96 | 8 | 32 | 54 | 24.33 | 0.1274 | 1 | 0.7212 |
| Male | 30 | 94.20 | 6 | 33 | 70 | 28.21 | | | |
| Female | 22 | 52.40 | 5 | 20.5 | 38 | 22.52 | 3.699 | 1 | 0.0544 |
| Age 2 | 17 | 43.18 | 6 | 22 | 47 | 13.45 | | | |
| Age 3 | 35 | 78.28 | 5 | 31 | 55 | 23.14 | 0.2926 | 1 | 0.5885 |
| Left site | 13 | 16.02 | 3 | 6 | 29 | 4.88 | | | |
| EstabHR | 25 | 94.29 | 9 | 31 | 54 | 30.61 | 15.3688 | 1 | **0.0001** |
| Homeward | 22 | 114.64 | 6 | 31.5 | 175 | 37.02 | | | |
| Not homeward | 30 | 36.37 | 5 | 22 | 41 | 8.20 | 11.21 | 1 | **0.0008** |

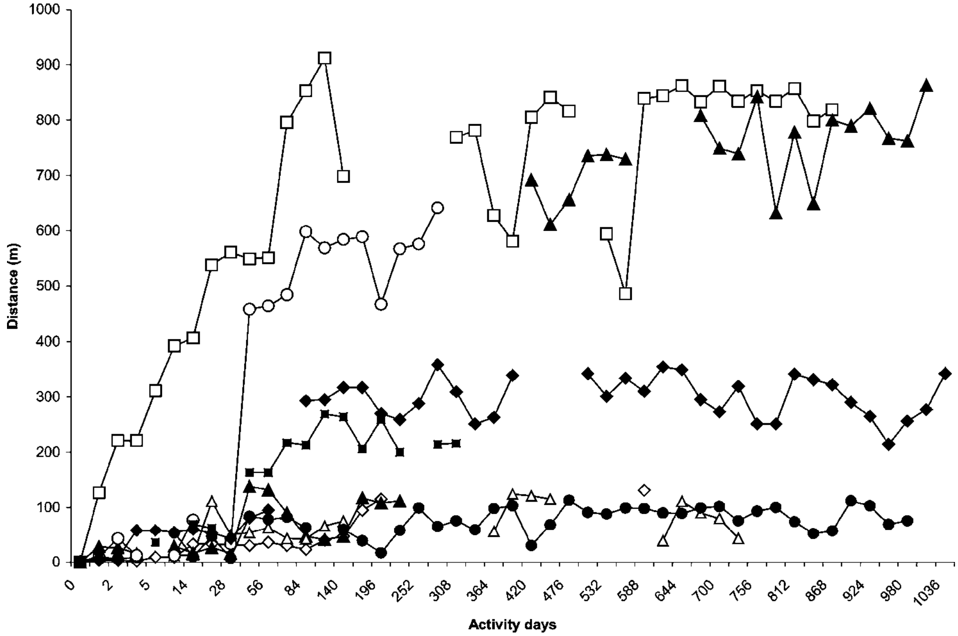

**Figure 3.** Straight line distance from release point, over time, for representative "pet" *T. carolina* translocated to Floyd Bennett Field. Individuals are: ◇ T320, □ T323, ▲ T356, △ T513, ● T313, ○ T332, ◆ T389, ■ T535.

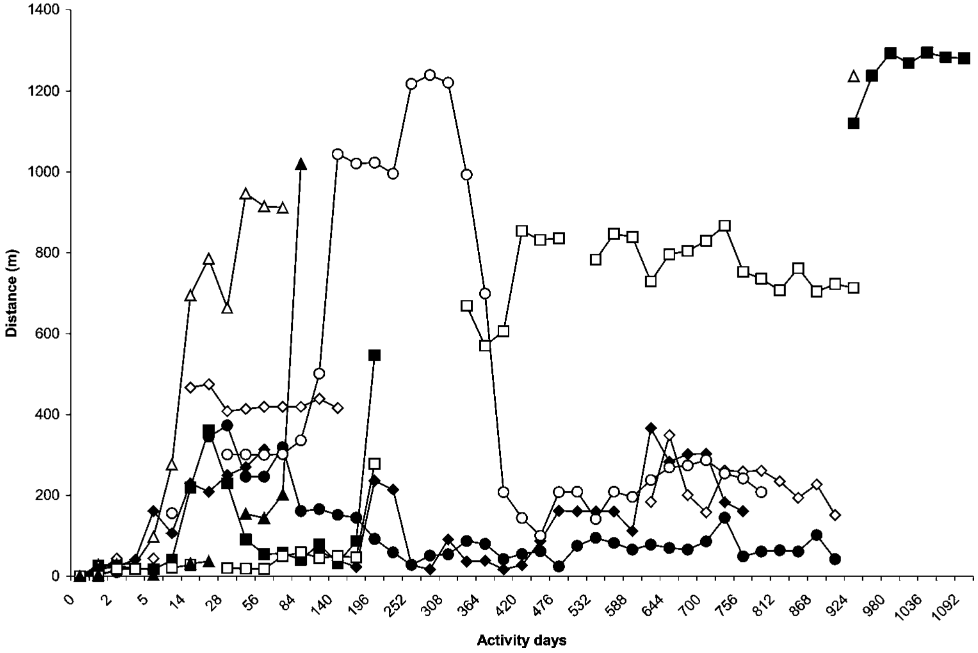

**Figure 4.** Straight line distance from release point, over time, for representative "wild" *T. carolina* translocated to Floyd Bennett Field. Individuals are: ◇ T261, □ T361, ▲ T512, △ T365, ● T271, ○ T355, ◆ T400, ■ T343.

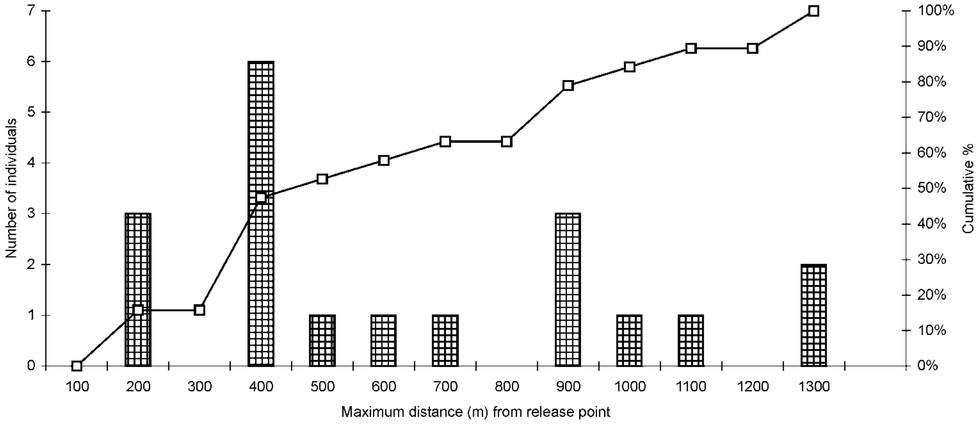

**Figure 5.** Frequency distribution of maximum distance from release point in 19 translocated *T. carolina* monitored at least two activity years.

672 activity days. Maximum recorded distance from the release point ranged from 113 to 1,295 m, with a mean of 592 m (SD = 370 and median = 475). Slightly more than 50% attained a maximum distance within 500 m (fig. 5). Time taken to reach maximum distance ranged from 21 to 1036 days, with a mean of 430 activity days (SD = 319 and median = 392 (fig. 6)).

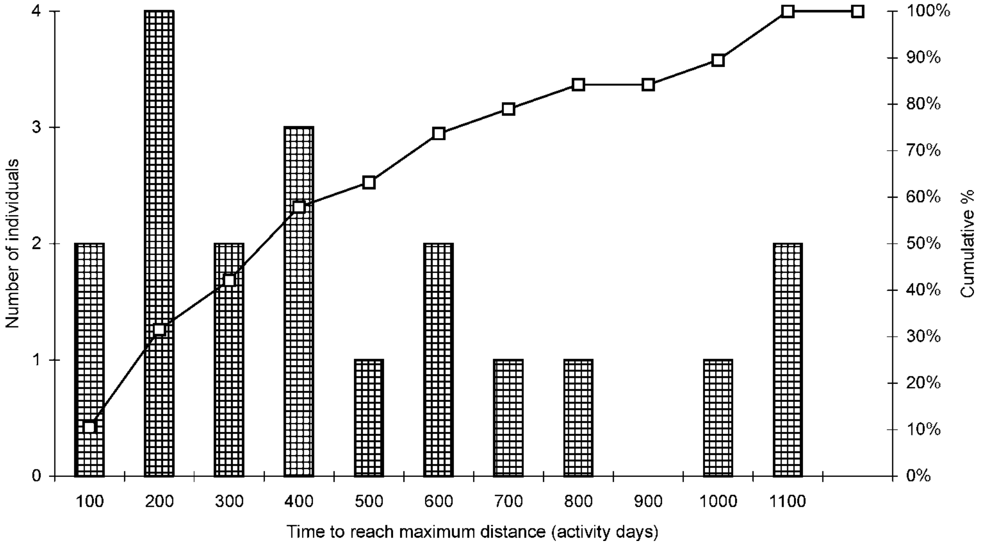

**Figure 6.** Frequency distribution of time taken to attain maximum distance from release point by 19 translocated *T. carolina* monitored at least two activity years.

Of the 53 radio-tagged *Terrapene*, 25 (47.2%) established home ranges, 13 (24.6%) left Floyd Bennett Field, and 15 (28.3%) died before establishing a home range or leaving the site. Of the 25 *Terrapene* that established home ranges, 17 (68%) did so in the release year, 2 (8%) in outyear one, 3 (12%) in outyear two, and 3 (12%) in outyear three. Animals that left the site were radio-tracked for a mean 49.4 days (range 4 to 85, SD = 31.7). Animals that died before an outcome could be determined were tracked for a mean of 149.7 activity days (range 6 to 322, SD = 102.0).

Mean home range did not vary due to sex or adult age class (table 2). Home ranges of detectably gravid females were significantly larger than non-gravid females and males, whilst home range of non-gravid females did not differ significantly from males (table 2).

Seventeen individuals (eight female, nine male) provided 25 inter-year comparisons of home range geographic centers. Fifteen comparisons showed a significant ($p < 0.05$) shift in home range center, with males accounting for eight instances and females seven. In the 10 instances of stability, males accounted for eight and females for two. Two males (T313 and T389) accounted for half of the instances of inter-year stability. While suggesting that males had greater home range stability, differences due to sex were not significant ($\chi^2 = 0.87$, df = 1, $p = 0.40$).

When inter-year shift was not significant, distance between home range centers ranged from 7.1 to 46.0 m (mean = 23.0, SD = 12.69). When inter-year shift was significant, this distance ranged from 16.5 to 202.9 m (mean 99.7, SD = 60.35). In the 15 instances of home range shift, there were no significant differences in magnitude of shift due to sex ($t = 1.04$, $p = 0.32$). Distance between consecutive

**Table 2.** Mean size (ha) of home ranges of translocated *T. carolina* that established home ranges. Analysis of age and sex based on two way ANOVA, other analyses one way ANOVA.

| | Mean | SD | Range | *n* | *F* | df | *p* |
|---|---|---|---|---|---|---|---|
| | | | 95% bivariate normal | | | | |
| Overall | 9.77 | 9.08 | 0.57-39.82 | 40 | | | |
| Male | 7.00 | 5.68 | 0.57-16.33 | 15 | | | |
| Female | 11.43 | 10.37 | 1.67-39.82 | 25 | 1.00 | 1,36 | 0.32 |
| Age 2 | 11.81 | 12.68 | 1.60-39.82 | 12 | | | |
| Age 3 + 4 | 8.90 | 7.144 | 0.57-33.32 | 28 | 0.02 | 1,36 | 0.90 |
| Gravid | 17.16 | 122.09 | 1.92-39.92 | 11 | | | |
| Non-gravid | 6.93 | 6.03 | 1.67-18.93 | 14 | 7.29 | 1,23 | 0.01 |
| Male | 7.00 | 5.68 | 0.57-16.33 | 15 | | | |
| Non-gravid | 6.93 | 6.03 | 1.67-18.93 | 14 | 0.02 | 1,27 | 0.88 |
| Male | 7.00 | 5.68 | 0.57-16.33 | 15 | | | |
| Gravid | 17.16 | 122.09 | 1.92-39.92 | 11 | 6.71 | 1,24 | 0.02 |
| | | | 95% harmonic means | | | | |
| Overall | 4.82 | 6.97 | 0.24-42.57 | 40 | | | |
| Male | 3.67 | 3.12 | 0.24-11.30 | 15 | | | |
| Female | 5.51 | 8.42 | 0.24-42.57 | 25 | 0.51 | 1,36 | 0.48 |
| Age 2 | 2.67 | 2.1 | 0.39-6.73 | 12 | | | |
| Age 3 + 4 | 5.74 | 8.09 | 0.24-42-57 | 28 | 1.16 | 1,36 | 0.29 |
| Gravid | 8.91 | 11.82 | 0.24-9.91 | 11 | | | |
| Non-gravid | 2.83 | 2.81 | 0.71-42.57 | 14 | 6.36 | 1,23 | 0.02 |
| Male | 3.67 | 3.12 | 0.24-11.30 | 15 | | | |
| Non-gravid | 2.83 | 2.81 | 0.71-42.57 | 14 | 0.27 | 1,27 | 0.60 |
| Male | 3.67 | 3.12 | 0.24-11.30 | 15 | | | |
| Gravid | 8.91 | 11.82 | 0.24-9.91 | 11 | 3.53 | 1,24 | 0.07 |

year's hibernacula varied between and within individuals, ranging from 0.3 to 332.1 m, with an overall mean of 97.6 m (SD $= 89.91$, $n = 44$) (table 3). Several individuals with small inter-hibernacula distances (e.g. T210, T310, T323, T389, T400, T489, T584) provide examples of hibernation site fidelity, hibernating in the same habitat patch in consecutive years. Though variable, most inter-hibernacula distances were less than 100 m. Turtle T389, which hibernated in essentially the same spot for five consecutive years, provides the best example of hibernation site fidelity. Yet, in the winter of 1993-94, it hibernated over 200 m from the site of the previous five winters, demonstrating the highly variable nature of this phenomenon.

Variability of inter-hibernacula distance was analyzed using SAS General Linear Model (Proc GLM). Neither individual turtles nor time periods were significant sources of variation ($p = 0.64$, and $p = 0.91$, respectively).

### *Survival, mortality, and persistence*

For the 32 radio-tagged individuals released in 1988, annual survival was 63%, 60%, 92%, 82% and 89% for the periods 1988-89, 1989-90, 1990-91, 1991-92 and 1992-

**Table 3.** Distance (m) between consecutive year's hibernacula in translocated *T. carolina*, by individuals and time period. For example, for Turtle 44, the hibernaculum used during winter 1992-93 was 106.2 m from that used in 1991-92.

| Turtle | H89-90 | H90-91 | H91-92 | H92-93 | H93-94 | H94-95 | Mean | *n* |
|---|---|---|---|---|---|---|---|---|
| 44 | | | | 106.2 | 97.3 | | 101.8 | 2 |
| 88 | | | | | 332.1 | | 332.1 | 1 |
| 210 | | | | 22.4 | | | 22.4 | 1 |
| 253 | | 51.2 | | | | | 51.2 | 1 |
| 261 | | | | | 190.5 | | 190.5 | 1 |
| 271 | | 237.8 | 22.6 | 44.7 | 98.9 | | 101.0 | 4 |
| 310 | | | | | | 12.2 | 12.2 | 1 |
| 313 | 53.6 | 102.3 | 63.6 | 70.1 | 43.1 | | 66.5 | 5 |
| 316 | 174.6 | | | | | | 174.6 | 1 |
| 323 | | | 5.0 | 5.0 | | | 5.0 | 2 |
| 332 | 140.3 | | | | | | 140.3 | 1 |
| 355 | | | 50.1 | | | | 50.1 | 1 |
| 356 | | | 20.1 | 233.5 | | | 126.8 | 2 |
| 361 | | | | 81.8 | | | 81.8 | 1 |
| 389 | 2.0 | 4.1 | 1.4 | 15.8 | 217.6 | | 48.2 | 5 |
| 400 | | 57.4 | 182.2 | 1.4 | | | 80.3 | 3 |
| 425 | | 265.8 | | | | | 265.8 | 1 |
| 489 | | | | 148.5 | 1.0 | | 74.8 | 2 |
| 502 | | | 150.0 | | | | 150.0 | 1 |
| 510 | | | 132.6 | | | | 132.6 | 1 |
| 524 | | | | | 132.6 | | 132.6 | 1 |
| 526 | | | | 16.0 | | | 16.0 | 1 |
| 528 | | | | 284.3 | 46.6 | | 165.5 | 2 |
| 540 | | | 204.7 | 170.5 | | | 187.6 | 2 |
| 584 | | | | | | 0.3 | 0.3 | 1 |
| Mean | 92.6 | 119.8 | 83.2 | 92.3 | 128.9 | 6.3 | 97.6 | |
| *n* | 4 | 6 | 10 | 13 | 9 | 2 | | 44 |

93, respectively. Survival in the 1989 and 1990 release-year cohorts was similar (fig. 7). For all release year cohorts combined, survival to the first spring after release was 70%, with annual rates over the next four years of 57%, 86%, 79% and 89%, respectively (fig. 8). The overall annual known survival rate and bounds of the 95% confidence interval was 71% (63% to 78%). While lowest rates of annual survival tended to occur within the first two years after release, annual survival rates were not significantly different ($\chi^2 = 7.66$, df = 4, $p = 0.11$). The annual survival rate for the first two years post-release was 64% (54% to 74%), and for years three to five it was 84% (70% to 92%).

Calendar year specific survival rates were 1988-1989, 63%; 1989-1990, 65%; 1990-1991, 80%; 1991-1992, 71%, and 1992-1993, 82%. Variation in calendar year specific survival rate was not significant ($\chi^2 = 3.991$, df = 4, $p = 0.45$).

Overall known survival to the third and fifth spring post-release was 35% and 25%, respectively (fig. 9). Differences in survival due to origin, time in acclimation

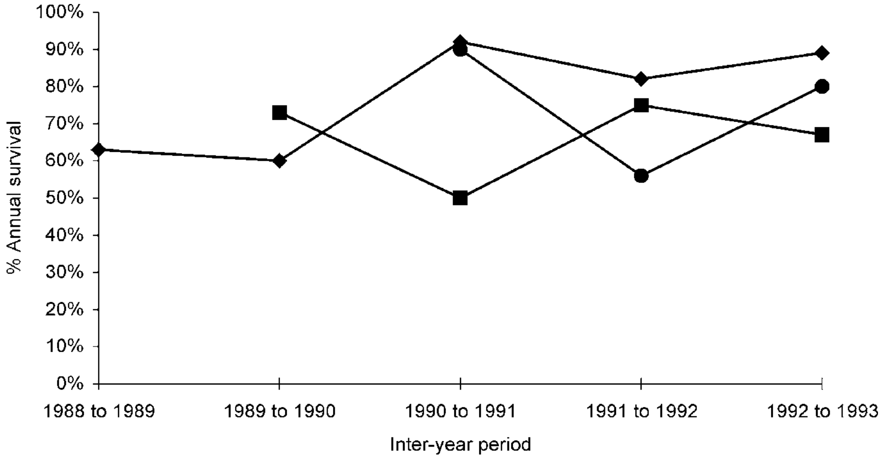

**Figure 7.** Annual survival of translocated *T. carolina* by release year (RY) cohorts. Solid diamond, 1988 RY, $n = 32$; solid square, 1989 RY, $n = 11$; solid circle, 1990 RY, $n = 10$.

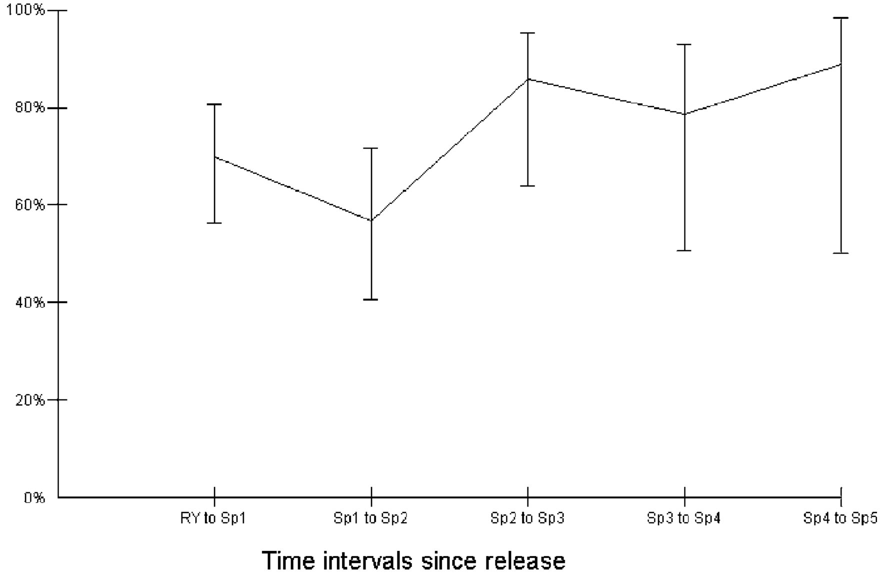

**Figure 8.** Annual rates and 95% confidence intervals for known survival, expressed as a function of time since release. Time intervals are release year (RY) to first spring (Sp1), etc. For the five successive time intervals, $n = 53, 37, 21, 14$ and 9, respectively.

pen, or sex were not significant. Survival in young adults (Age Class 2) was lower than older adults (Age Class 3 + 4) (table 4). At three springs post-release these differences were significant. Proportional hazards regression found no significant differences in time to death/disappearance due to origin ($\chi^2 = 0.003$, df $= 1$, $p = 0.96$), time in acclimation pen ($\chi^2 = 0.007$, df $= 1$, $p = 0.94$), or sex

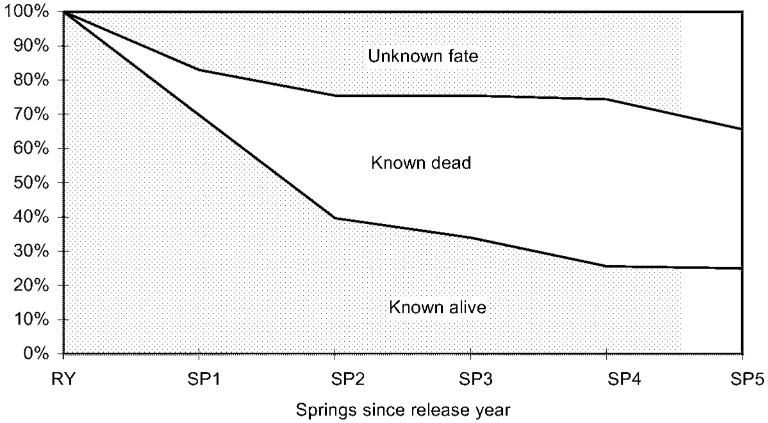

**Figure 9.** Fate of radio-tagged *T. carolina* translocated to Floyd Bennett Field. Time expressed as springs since release year. SP1, SP2 and SP3, $n = 53$; SP4, $n = 43$, and SP5, $n = 32$.

**Table 4.** Known survival of radio-tagged *T. carolina* to 3 and 5 years post-release (by origin, time in holding pen, sex, and age). Percent of individuals released still alive after 3 and 5 years.

| | Survival to 3 years after release | | |
|---|---|---|---|
| | Wild ($n = 27$) | Pet ($n = 26$) | $\chi^2$ |
| Origin (wild or pet) | 33% | 35% | 0.04 |
| | 0 days ($n = 29$) | 15 days ($n = 24$) | |
| Holding Pen (0 or 15 days) | 34% | 33% | 0.04 |
| | Male ($n = 30$) | Female ($n = 23$) | |
| Sex (M or F) | 37% | 30% | 0.03 |
| | Age Cat 2 ($n = 17$) | Age Cat 3,4 ($n = 36$) | |
| Age (Category 2 or Category 3,4) | 6% | 47% | 7.05* |
| | Survival to 5 years after release | | |
| | Wild ($n = 15$) | Pet ($n = 17$) | $\chi^2$ |
| Origin (wild or pet) | 27% | 24% | 0.04 |
| | 0 days ($n = 17$) | 15 days ($n = 15$) | |
| Holding Pen (0 or 15 days) | 24% | 27% | 0.04 |
| | Male ($n = 17$) | Female ($n = 15$) | |
| Sex (M or F) | 35% | 13% | 1.05 |
| | Age Cat 2 ($n = 10$) | Age Cat 3,4 ($n = 22$) | |
| Age (Category 2 or Category 3,4) | 0% | 36% | 3.1 |

* Significant at the $p = 0.01$ level.

($\chi^2 = 0.0000$, df = 1, $p = 0.998$), but differences due to age were significant ($\chi^2 = 5.563$, df = 1, $p = 0.018$).

Age-related differences in known survival may be due to differences in known mortality and/or unknown fates. For young and old adults, respectively, known mortality after three years was 47% and 39%. After five years, it was 30% and

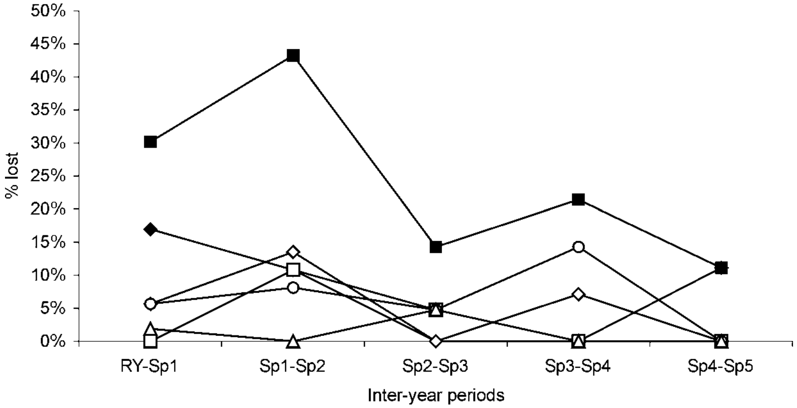

**Figure 10.** Annual percent loss of translocated *T. carolina* at Floyd Bennett Field to different factors. Loss expressed as percentage of total number of radio-tagged individuals alive at beginning of each inter-year period. For the five successive time intervals, $n = 53, 37, 21, 14$ and 9, respectively. Factors are: all ■; pneumonia □; winter kill ◇ ; unknown mortality ○; vehicle △; unknown fate ◆ .

45%. Age-related differences in known mortality were not significant after three years ($\chi^2 = 0.07$, df = 1, $p = 0.81$) nor five years ($\chi^2 = 0.19$, df = 1, $p = 0.89$). However, "fate unknown" after three years was 47% and 15% of young and old adults, respectively. After five years it was 70% and 23%. Age-related differences in "fate unknown" were significant after three years ($\chi^2 = 5.18$, df = 1, $p = 0.02$) and five years ($\chi^2 = 6.05$, df = 1, $p = 0.01$).

Annual percent loss of individuals to unknown fate (most of whom likely left the site) and known mortality was greatest in the first two years after release (fig. 10). Causes of known mortality were winter kill (31%), unknown cause (31%), pneumonia (19%), and vehicles (12%). Winter kill varied. Percentage of hibernating individuals that did not survive were 5%, 38%, 5%, 7.5%, and 0% for the winters of 1988-89, 1989-90, 1990-91, 1991-92, and 1992-93, respectively.

### *Reproductive output*

There were 19 records of gravid females (table 5). These show considerable variation in reproductive effort. Some individuals were gravid in all years for which data exist (e.g. T528) whereas others (e.g. T400, T489, T526, T540) never were. Others were gravid in some, but not all years. In 1993, 7 of 15 (47%) of females were gravid. Mean clutch size was 5.8 (range 1 to 9) (SD = 2.23, $n = 11$). The relationship between clutch size and carapace length ($r = 0.11$, $p = 0.74$) was not significant. Total annual reproductive output in FBF *T. c. carolina* in 1993 was 2.74 eggs adult female$^{-1}$ ((0.47 clutches female $^{-1}$) × (5.68 eggs clutch $^{-1}$)).

A total of ten offspring was recorded (table 6), indicating that some *Terrapene* were reproducing by 1988. Most records (8 of 10) were of individuals at least three years post-hatching, and occurred in or after 1993. Of the eight individuals recorded from 1993 through 1995, five were found by "Gus", the Labrador retriever.

**Table 5.** Fecundity rates and annual variation in reproductive effort in female *T. carolina* translocated to Floyd Bennett Field (yes = gravid, no = not gravid).

| Turtle | 1990 | 1991 | 1992 | 1993 | 1994 | 1995 | Fecundity |
|---|---|---|---|---|---|---|---|
| 18 | | | no | | | | 0% |
| 44 | | | no | yes | | | 50% |
| 72 | | | | yes | | | 100% |
| 74 | | | yes | | | | 100% |
| 88 | | | | yes | | | 100% |
| 92 | | | | no | yes | | 50% |
| 210 | | | yes | no | yes | | 67% |
| 310 | | | | yes | | | 100% |
| 341 | | | | yes | | | 100% |
| 348 | | | | yes | | | 100% |
| 351 | | | | no | yes | yes | 67% |
| 400 | | no | no | | | | 0% |
| 412 | | | | no | | | 0% |
| 466 | | | | no | | | 0% |
| 489 | | | no | no | | | 0% |
| 502 | | | no | | | | 0% |
| 505 | | | | | | yes | 100% |
| 512 | no | | | | | | 0% |
| 513 | | | yes | | no | | 50% |
| 524 | | | no | | | | 0% |
| 526 | | | no | no | | | 0% |
| 528 | yes | | yes | yes | | | 100% |
| 532 | | | no | | | | 0% |
| 540 | | | no | no | | | 0% |
| Inds gravid | 1 | 0 | 4 | 7 | 3 | 2 | |
| Inds total | 2 | 1 | 13 | 15 | 4 | 2 | |
| Annual rate | 50% | 0% | 31% | 47% | 75% | 100% | 46% |

**Table 6.** Hatching year (HY) and year first recorded (YFR) for young *T. carolina* on Floyd Bennett Field.

| Hatch | Year first recorded | | | | | | Total |
|---|---|---|---|---|---|---|---|
| year | 1990 | 1991 | 1992 | 1993 | 1994 | 1995 | by HY |
| 1988 | 1 | | | | | 1 | 2 |
| 1989 | | | 1 | | 1 | | 2 |
| 1990 | | | | 2 | | 2 | 4 |
| 1991 | | | | | | | 0 |
| 1992 | | | | 1 | | 1 | 2 |
| 1993 | | | | | | | 0 |
| 1994 | | | | | | | 0 |
| 1995 | | | | | | | 0 |
| Total by YFR | 1 | 0 | 1 | 3 | 1 | 4 | 10 |

## Discussion

### *Dispersal and home range*

For many species, the ability to home is a serious concern, potentially limiting translocation success (Berry, 1986; Diemer, 1989). From a translocation perspective, homing has two aspects: direction and duration. While direction may be important, duration is probably more critical. If homing were to persist indefinitely, successful translocation would be unlikely.

The general but highly variable homing tendency displayed by the *Terrapene* translocated to Floyd Bennett Field is consistent with most literature on this subject (Gould, 1957, 1959; Lemkau, 1970; Madden, 1975; Nichols, 1939). For long distance translocations, the results here are intermediate between those of Hall (1987) who reported no significant homeward orientation, and the highly directed homing response obtained by DeRosa and Taylor (1980) in pen trials. Vector length ($r = 0.234$) and home component (hc = 0.214) obtained in this study are low compared to those of De Rosa and Taylor (1980) ($r = 0.642$, hc = 0.582) and Lemkau (1970) ($r = 0.41$, hc = 0.362).

Though homing occurred, it was weak, and appears unrelated to home range establishment or dispersal. Of 20 individuals that homed, 16 established home ranges and four dispersed. Of 18 individuals that did not home, 9 established home ranges and 9 did not. These frequencies did not differ from random (Fisher exact test, $p = 0.09$). That individuals establishing home ranges also tended to be significantly orientated homeward indicates that homing frequently did not persist *ad infinitum*. While it would not be reasonable to suggest that homing led to home range establishment, homing certainly did not necessarily lead to dispersal from the site.

The pattern of variation in dispersal speed observed appears typical of *T. carolina*. Other Long Island *T. carolina*, relocated relatively short distances, took from 0 to 14 days (mean 2.2) to disperse 50 m, with 82% doing so in four days (Madden, 1975). Williams and Parker (1987) also noted considerable variation in individual dispersal speeds after short distance relocations, averaging from 10 to 421 m day$^{-1}$ (mean 74.7). Data from Lemkau (1970), however, provided less variable estimates of average dispersal speed, ranging from 71 to 171 m day$^{-1}$.

While there were no significant differences in initial dispersal speed due to age, sex, origin, or pre-release treatment, there were significant differences relative to homing and home range establishment. Individuals that dispersed homeward took significantly longer to reach the 100 m radius, indicating that rapid initial dispersal was not associated with homeward orientation. Moreover, individuals that left the release site had a significantly greater dispersal speed than individuals that established home ranges (table 1). Hall (1987) also reported rapid, non-homeward uni-directional movement in *Terrapene* translocated long distance (28 km), and Kiester et al. (1982) also report “transients” moving continuously in one direction.

The maximum recorded distance dispersed, 1295 m, is less than the up-to-several kilometer movements reported in other studies of *Terrapene* (Doroff and Keith, 1990; Kiester et al., 1982). Due to tracking failures and the peninsular nature of FBF, there was some bias against high values (Cook, 1996). In a continuous landscape with no tracking failures, the data would likely show greater maximum distances, and proportionately more individuals with high values. In spite of these limitations, the data accurately reflect the fact many individuals did not disperse great distances, even after three to five years.

Based on these analyses, a general model of post-release dispersal of translocated *T. carolina* emerges. Though individually variable, *T. carolina* tended to disperse homeward. Individuals taken directly from the wild and released within a few days show no greater homeward tendency than individuals held a minimum of 15 days on or off site prior to release. Homing was not associated with rapid initial dispersal or dispersal from the site, nor did it persist indefinitely. Most individuals eventually established home ranges. Individuals that left the site tended towards rapid initial dispersal. Individuals that dispersed rapidly also tended to disperse greater distances. The majority of individuals remained within a kilometer of the release point, but many dispersed further, and in a continuous landscape would have dispersed even further.

Reserve size is an important issue in conservation and the subject of extensive research (reviewed by Shafer, 1990). For translocated animals, size of release site is critical, often determining persistence or “settling rates”. Translocated animals may home or engage in other linear movements (Berry, 1986; Hall, 1987), and distances traveled are often greater than those of animals on their original home range (Doroff and Keith, 1990). For translocation to succeed, animals must remain on the release site in sufficient numbers and density to reproduce.

In rural and wildland landscapes, reserves may be buffered by similar habitats and compatible land use. Hence the actual available habitat may be larger than administrative boundaries of a release site. However, as fragmentation and urbanization increase, buffers are lost and effective reserve size is reduced to that of the reserve alone and eventually even further, due to edge effects (Lovejoy et al., 1986). In this discussion, a release site is considered a habitat island.

For the *T. carolina* translocated to FBF, data on maximum distance from release point were used to estimate reserve size required to retain increasing proportions of individuals. Assuming a circular shape (since animals dispersed in all directions) and radius equal to the maximum distance (1295 m), an area of 527 ha (1302 acres) is needed to retain 100% of the individuals. An area of 100 ha (247 acres) retained 55% of individuals, and 300 ha (741 acres) retained 83% of individuals. These estimates, which are conservative due to the bias towards short dispersal distance discussed above, indicate that reserves for translocated *T. carolina* need to be at least 300 ha to retain most individuals.

Home range establishment is one of the first in a sequence of events necessary for translocation to succeed. Data on rates of home range establishment or “settling behavior" (Berry, 1986) are few. In *G. agassizii*, settling rates ranging from 30 to 50% have been reported (Berry, 1986), though some of these are based on relatively short term monitoring (e.g. a month). Settling rates in *G. polyphemus* appear to vary according to release site size and habitat quality. They range from 100% on a large (259 ha) site (Fucigna and Nickerson, 1989) to rates in the 30% to 60% range on smaller (16 to 60 ha) sites (Burke, 1989; Godley, 1989; Stout, 1989). Due to variation in size and quality of release site, as well as the duration and methodology of monitoring, settling rates are hard to compare. Animals dispersing "off site" may settle beyond the limits of the area studied, or may die, if dispersing from a habitat island into unsuitable habitat.

While home range establishment by translocated *Terrapene* has been documented (Metcalf and Metcalf, 1970; Nichols, 1939; Schwartz and Schwartz, 1974), these works do not provide settling rates. In Wisconsin, *T. ornata* settling rates ranged from ca. 40% for animals released directly (Doroff and Keith, 1990) to 100%, for animals held two years on-site in a one ha. pen prior to release (Hatch, 1996). The 47% settling rate in the *Terrapene* translocated to FBF is comparable to that found in most studies of *Gopherus*, and corresponds closely to Landers (1981) recommendation that *G. polyphemus* translocation programs should plan on a 50% settling rate.

Home range size has been studied in many populations of *T. carolina* (Dolbeer, 1969; Madden, 1975; Nichols, 1939; Schwartz et al., 1984; Stickel, 1989; Strang, 1983; Williams and Parker 1987). Though these studies vary in duration, sample size, and method of calculating home range, they concur regarding magnitude of home range size, home range stability, and patterns of variation due to sex and age. These works, as well as those on *T. ornata* (Legler, 1960; Doroff and Keith, 1990), generally conclude that home range size is not significantly affected by sex, with juveniles and sub-adults having smaller home ranges than adults, and adult home ranges tend to be stable in size and location over time. Variation in home range size at both the inter- and intrapopulation level appears attributable to habitat quality and diversity (patchiness), with diverse, high quality habitat correlated with small home ranges (Madden, 1975; Stickel, 1989).

Home range size of *T. carolina* at FBF exceeded other accounts, though methodological differences make some comparisons less useful. The mean 95% bivariate normal home range, 9.77 ha, is larger than the 6.96 ha reported for another Long Island population (Madden, 1975), and considerably larger than in Maryland bottomland forest, where males averaged 1.20 ha and females 1.13 ha (Stickel, 1989). Differences in home range size on Long Island *vs* Maryland were attributed to differences in habitat quality (Madden, 1975), and in general, inter-populational differences in home range size are believed to reflect population density and habitat quality (Stickel, 1950, 1989). Based on Stickel's long term work, box turtle density increases and home range size decreases as habitat quality increases, and mature, bottomland forest was considered higher quality habitat than drier forest or more open habitats.

Compared to the study sites of Madden and Stickel, as well as others cited above, FBF is lower quality habitat. Due to its recent creation, shrub and woodland habitat is patchy. Moving from patch to patch through less preferred open habitats (Reagan, 1974), results in larger 95% bivariate normal home ranges. The mean 95% harmonic mean estimate, 4.82 ha, is half of the bivariate normal. This difference is consistent with harmonic means better reflecting actual area used. Even the 95% harmonic mean estimate (4.82 ha) however, reflects FBF's lower habitat quality, exceeding Madden's 1.76 ha estimate of actual utilized home range.

Though home range size was greater for FBF *T. carolina*, patterns of variation were similar to other populations. The variability in home range size, 0.57 to 39.82 ha (bivariate normal) and 0.24 to 42.57 ha (harmonic mean), is comparable to other populations; 0.6 to 10.6 ha (Schwartz et al., 1984), 1.4 to 19.2 ha (Madden, 1975), 0.02 to 2.63 ha (Dolbeer, 1969), and 0.21 to 28.02 ha (Williams and Parker, 1987). The lack of significant differences in home range size due to sex or age (young adult versus older adult) is consistent with other populations of *Terrapene* (Legler, 1960; Dolbeer, 1969; Madden, 1975; Schwartz et al., 1984; Stickel, 1989; Doroff and Keith, 1990). The larger home ranges of gravid females is consistent with reports that nesting forays often take females to areas beyond their "normal" home range (Williams and Parker, 1987; Stickel, 1989). Thus, while there may not be any inter-sex differences in the amount of area required to meet energy requirements and general needs, larger areas may be needed to provide specialized requirements such as nesting habitat.

The extent to which nesting requirements increase home range in *T. carolina* is site dependent. Stickel (1989) indicated that females extended their home ranges by leaving bottomland forest to nest in drier and warmer upland sites. On the other hand, Madden (1975) concluded that most females nested at sites within their home range. In this case, habitats were more mesic and patchy than those of Stickel, and the home range size reported by Madden is five times that reported by Stickel. Given the larger home range size and greater habitat heterogeneity at the Long Island site of Madden, there would be less need for a nesting foray. This would suggest that at FBF, with its patchy habitat, females would not need to travel far to nest. This apparent contradiction may be due to the fact that females tend to return year after year to nest in the same area (Stickel, 1950, 1989; Madden, 1975), indicating that prior experience plays a role in nesting movements. Translocated turtles lack this prior experience, and presumably search more extensively.

Though Nichols (1939) reported that some individuals may shift home range over the years, most adult *Terrapene* tend to have stable home ranges (Legler, 1960; Schwartz et al., 1984; Doroff and Keith, 1990). Rates of home range stability (i.e. no significant inter-year shift in home range geographic center) reported for populations of *T. c. carolina* are 88.2% (Yahner, 1974), 87.5% (Madden, 1975), 89.8% of females and 86.8% of males (Williams and Parker, 1987). Stickel (1989) found no significant shift in the geographic centers of home ranges in 63% of inter-year comparisons. Where differences were statistically significant, the actual shift in geographic center (mean 59 m, range 17 to 124 m) was still relatively small.

Home ranges of *T. carolina* at FBF were less stable. Only 40% of inter-year comparisons were non-significant. Though more inter-year shifting is occurring at FBF, the magnitude of the shifts (mean 100 m, range 17 to 203) is similar to the results of Madden (1975) and Stickel (1989). The greater amount of inter-year shifting at FBF is likely due its patchier habitat, but may also indicate that home ranges are not as firmly established as in non-translocated populations.

Fidelity to hibernation sites has been documented in *T. ornata* (Metcalf and Metcalf, 1979; Doroff and Keith, 1990), *T. c. triunguis* (Carpenter, 1957), and *T. c. carolina* (Madden, 1975; Stickel, 1989; Claussen et al., 1991). In the most detailed of these works, Carpenter (1957) concluded there was "great variation in the tendency and/or non-tendency of individuals to return to hibernacula". Collectively, these works indicate that some individuals consistently use the same hibernation site, others generally do, but occasionally skip a year, and others are less predictable.

Patterns of inter-hibernacula distances of FBF *Terrapene* (table 4) are similar to those reported by Carpenter (1957), though the mean distance on FBF (97.6 m) is twice that reported by Carpenter (49.4 m). However, the site studied by Carpenter (1957) was nearly all woodland and less patchy than FBF. Overall, patterns of hibernation site fidelity in FBF *Terrapene* are similar to those of naturally-occurring populations, suggesting they are familiarizing themselves with the site and behaving similar to non-translocated animals.

### *Survival, mortality, and persistence*

Annual survival in *T. carolina* generally ranges from 85% to 95%, with long term annual rates estimated at 93.3% (Stickel, 1978), 89% (Schwartz and Schwartz, 1991), and 93.2% (Williams and Parker, 1987). Survival of *T. carolina* translocated to FBF was lower. However, some patterns of variation, such as lower survival of young adults (Age Class 2), are consistent with the results of Williams and Parker (1987) and Schwartz and Schwartz (1991). Though inter-year differences in survival rates were not statistically significant, survival tended to be lowest the first two years after translocation (fig. 8) and "mortality" greatest (fig. 10). The question of whether survival or retention rates increase after the first two years post-release is discussed by Seigel and Dodd (2000), who point out that there are no data demonstrating it. While my data lack statistical significance, the slight overlap in 95% confidence limits of the first two and last three year's survival rates suggest that survival increased after the initial two years.

In evaluating known survival, it is useful to look at its converse, "mortality", which includes known mortality, known dispersal, and animals of unknown fate. Most animals classified as unknown fate were unaccounted for after the first year or two (fig. 9), indicating that this mortality factor operates principally in the first couple of years after release. Animals of unknown fate may have dispersed from the site, or may still be present on site, either dead or alive. Of these possibilities, dispersal from the site probably accounts for most (Cook, 1996).

Williams and Parker (1987), and Schwartz and Schwartz (1991) report that 25% of the turtles they marked were never recaptured. They described these individuals as transients, individuals that were passing through the site, exhibiting long term uni-directional movement (Kiester et al., 1982; Schwartz et al., 1984). If populations of *T. carolina* consist primarily of sedentary individuals with established home ranges and lesser numbers of transients (Schwartz (2000) reports a 3:1 ratio), animals collected for translocation would include, and perhaps be biased towards, transients, since individuals were often collected while crossing roads. Also consistent with the idea that most of the fate-unknowns have left the site is the high rate of unknown fate in young adults. Both Williams and Parker (1987) and Schwartz and Schwartz (1991) report that younger adults show a greater tendency to disperse from the site. Moreover, the relationships found here between homing and home range establishment are also consistent with a situation in which most individuals collected from a home range dispersed in a homeward direction and eventually re-established a new home range. Conversely most individuals that left FBF (9 of 13) were not homeward oriented, and as transients or young adults, would have no home range to orient towards. Similar results have been reported in translocated *G. polyphemus*, in which all of the 57.4% "mortality" in two years following release was due to animals leaving the release site, with most occurring in the first year (Burke, 1989).

The second component of demographic mortality is known mortality. Similar to fate unknowns, most known mortality occurred within two years of release, suggesting that it is also dominated by factors operating primarily in the first couple of years. Predominant causes of known mortality were winter-kill, unknown causes, and pneumonia. Half the deaths attributed to unknown causes were individuals missing due to radio failure and subsequently recovered as skeletal remains. Since winter-kill and pneumonia were the two largest identified sources of mortality, presumably some of these unknown individuals died from these causes.

Eight of nine cases of winter kill occurred within the first two winters after release. Whilst this might suggest that individuals recently released were unable to find adequate hibernacula, the fact that five of eight cases occurred in the second rather than first winter suggests otherwise. Also affecting winter mortality is year-specific weather. Winter mortality for winter 1989-90 was 38.5%, and accounted for 56% of all recorded winter mortality. Of the five individuals that died that winter, three had survived the previous winter. Considering that December 1989 included an extremely severe early cold snap (Cook, 1996), when overwintering turtles are still relatively shallow (Dolbeer, 1971; Congdon et al., 1989; Claussen et al., 1991), severe early winter weather seems the most plausible explanation for high mortality in the winter of 1989-90.

Most deaths from pneumonia (four of five) occurred between the first and second year after release. Individuals affected had creamy nasal discharges (Evans, 1983) and experienced gradual weight loss prior to death. Transmission of disease is a major concern in translocations, with respiratory diseases of turtles being a particularly acute problem (Berry, 1986; Jacobson et al., 1995). These observations suggest that disease transmission occurred during the transportation to and/or penning at FBF and that it took a couple of years to run its course. Thus, mortality associated with pneumonia occurs relatively soon after release, and diminishes thereafter.

The lower survival that occurred in the first two years following release (70% and 57%) is most plausibly seen as the result of losses due to dispersal from release site and pneumonia (both of which were greatest initially), plus a random event, a severe cold snap in December of 1989. This event was within two years of the release of 81% (43/53) of all radio-tagged turtles, and killed 9.4% (5/53) of the radio-tagged turtles released. Following these initial two years, annual survival of radio-tagged turtles increased, ranging from 79% to 89%. While annual survival over the first two year's post-release period was 64%, even the annual survival over the last three years, 84%, is nearly 10 percentage points below the ca. 93% long term average annual survival reported for *T. c. carolina* in Maryland and Indiana (Stickel, 1978; Williams and Parker, 1987). While my estimates of known survival are conservative, and actual survival may be slightly greater, survival of the *T. carolina* translocated to FBF was less than in natural populations.

Relatively low rates of known survival or "persistence" are typical of translocation efforts involving *G. agassizii* and *G. polyphemus* (Berry, 1986; Diemer, 1989). In one translocation of *G. polyphemus* to a 40 ha site, persistence to two years post-release was 42.6%, corresponding to annualized rate of 65.5%. No actual mortality was reported. All losses were from dispersal in the first year (Burke, 1989). In another *G. polyphemus* translocation, mean survival time of translocated turtles (22 months) was considerably less than that of residents (53 months). Seventy percent of repatriated turtles were never recaptured, compared to 45% of residents, with most loss occurring in the first year after release. After the first year, however, remaining translocated turtles actually had a slightly higher survival (Layne, 1989). The results here parallel those with *Gopherus* in demonstrating the contribution of off-site dispersal to overall survival or persistence, though for FBF *Terrapene*, dispersal from the release site was less, and disease and winter kill correspondingly more important.

### *Reproductive output*

Chelonians vary in annual reproductive output and its components, clutch size and frequency, due to size, latitude, age at maturity, and longevity (Iverson, 1992). In addition, spatial and temporal variation in availability of energy resources also appears important (Dodd, 2001). Thus, reproductive output reflects the interaction of intrinsic and extrinsic factors. Reproductive data for *Terrapene* are limited, and often based on different methods, and for different species, subspecies, and geographic regions, under different conditions (e.g. captive *vs in situ*). This further complicates interpretation. Obtaining reliable data on reproductive output in the wild requires intensive sampling or radio-tracking of females in a population over the course of a nesting season in conjunction with X-ray. Few such data exist.

*Terrapene* conform to the generalization (Iverson, 1992) that southern animals have smaller but more frequent clutches than northern (Dodd, 2001). Thus mean clutch size in *T. carolina* increases from south to north; 2.4 for Florida *T. c. bauri* (Dodd, 1997), 3.4 for captive Louisiana *T. c. triunguis* (Messinger and Patton, 1995), 3 (mode) in North Carolina *T. c. carolina* (Stuart and Miller, 1987), 3.6 in captive Washington, D.C., *T. c. carolina* (Ewing, 1935), 6.7 in Connecticut *T. c. carolina* (Klemens, 1993), and 5-7 in Illinois *T. c .carolina* (Cahn, 1937). The mean clutch size of FBF *T. c. carolina* (5.8) is consistent with this pattern.

Data on clutch frequency and annual reproductive output are few, and difficult to interpret. Based on follicle counts, Kansas *T. ornata* produced at least one clutch and a third of them a second, giving a mean clutch frequency of 1.33 clutches female$^{-1}$ and annual output of 6.25 eggs female$^{-1}$ (Legler, 1960). In contrast, Doroff and Keith (1990), using radio-tracking *in situ* and X-rays, found no evidence of double clutching, a mean clutch frequency of 0.57 and annual output of ca. 2 eggs female$^{-1}$ in Wisconsin *T. ornata.* In Florida *T. c. bauri*, over a four year period, a minimum of 13.7% to 41.4% of females were gravid in any year (mean 27%). Individual clutch frequency ranged from zero to three clutches year$^{-1}$, but population average was 0.304 clutches female$^{-1}$ year$^{-1}$ and output was 0.72 eggs female$^{-1}$ year$^{-1}$. However this represents a minimum estimate, and probably reflects diminished output due to limited resources (Dodd, 1997, 2001). Captive *T. c. triunguis* in Louisiana produced 3.31 clutches year$^{-1}$ and 11.25 eggs female$^{-1}$ (Messinger and Patton, 1995) and, for captive *T. c. carolina* near Washington, D.C., clutch frequency was 1.14 clutches female$^{-1}$ and annual output was 4.1 eggs female$^{-1}$ (Ewing, 1935).

The annual reproductive output of FBF *T. c. carolina* in 1993 (2.74 eggs female$^{-1}$) exceeds estimates for wild populations of *T. ornata* (2 eggs female$^{-1}$) (Doroff and Keith, 1990) but is less than estimates from captive populations of *T. c. carolina* in Washington, D.C., 4.1 eggs female$^{-1}$ (Ewing, 1935). Though New York *T. c. carolina* would be expected to have greater annual output than populations from Washington, D.C., Ewing's captive population likely represents enhanced reproductive output. While it is possible that resource availability may be a limiting factor at FBF, the reproductive output of the *T. c. carolina* translocated there is reasonably consistent with what would be expected in a nearby natural population. In addition, individual patterns of annual reproduction of FBF *T. c. carolina* (table 5) are similar to those reported in *T. ornata* (Doroff and Keith, 1990) and *T. c. bauri* (Dodd, 1997).

The ten progeny records indicate that some successful nesting and hatchling survival is occurring. The concentration of records in recent years (table 6) reflects a process where young produced in the early years reach an age and size where they become more readily observed, plus the increased ability to find turtles using a dog. During the years when a dog was used (1993-1995), five of eight young turtles recorded were found by the dog. Overall, these data show that *Terrapene* on FBF are encountering mates, and producing eggs and offspring that survive beyond the hatchling stage. While comparisons with other populations require some interpolation, the results suggest that reproductive output is comparable to wild populations of *Terrapene*, and in conjunction with the increasing numbers of young recorded, suggest there is a growing population of FBF-native *Terrapene*.

## Conclusions

For the *T. carolina* repatriated to FBF, many of their patterns of behavior and population parameters were similar to those of wild *Terrapene* populations, suggesting that the translocated animals are settling in and becoming established. Indeed, roughly half of them established home ranges, and increasing numbers of juveniles were being found. These are important steps in the process of population establishment, though production of young in itself does not define translocation success (Seigel and Dodd, 2000). Home range establishment, production of young, and increasing survival rates are encouraging signs, but it is too soon to know if a viable population has been established. Additional data, and further analysis will be necessary to project long term population viability.

Short term results do confirm that many of the issues affecting translocation success in *Gopherus* (Berry, 1986; Diemer, 1989) apply to *Terrapene* as well. While homing occurred, it had little effect on off-site dispersal, which seems more related to the presence of transients (up to 25% of individuals in a population (Schwartz, 2000)). Size of release area, was also an important issue. Given the existence of transients, plus animals homing, even 575 ha FBF was unable to retain all the translocated individuals. Moreover, disease, i.e. pneumonia, was initially a problem. An acclimation pen, while having no effect on dispersal, may contribute to pneumonia transmission, and should be avoided. Clearly, survival or “persistence” was strongly influenced by the inter-related factors of dispersal and release site size, as well as disease, particularly in the years immediately following release.

While it is too soon to know the ultimate outcome of this translocation, the results demonstrate that any program to translocate *T. carolina* must recognize and have strategies to deal with the three major issues associated with turtle translocation; dispersal, genetic incompatibility, and disease (McDougal, 2000). Translocation is hardly a panacea (Dodd, 2001). Significant numbers of animals will not survive the process, due to dispersal and disease. While those that do survive establish home ranges and reproduce, the ultimate viability as a population will depend on the numbers released and size of release site. Based on this work, release sites need to be several hundred hectares to retain translocated individuals. Sites this size, consisting of appropriate habitat and lacking existing populations of *T. carolina* are few: FBF represents an unusual situation in this respect. Thus, while translocation may have some potential for establishing populations of *T. carolina* in extremely limited situations, given the many challenges to its success, and its limited applicability, I would concur with Seigel and Dodd's (2000) view of its being an unproven technique that should be considered as a last resort.

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