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MOVEMENT AND ECOLOGY OF EASTERN BOX AND PAINTED TURTLES REPATRIATED TO HUMAN-CREATED HABITAT.

by

ROBERT P. COOK

A dissertation submitted to the Graduate Faculty in Biology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York.

1996

UMI Number: 9630452

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This manuscript has been read and accepted for the Graduate Faculty in Biology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

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Abstract

MOVEMENT AND ECOLOGY OF EASTERN BOX AND PAINTED TURTLES REPATRIATED TO HUMAN-CREATED HABITAT

by

Robert Peter Cook

Advisor: Professor Max K. Hecht

The feasibility of repatriation as an approach to conservation and population restoration in the eastern box turtle (Terrapene c. carolina) and the eastern painted turtle (Chrysemys p. picta) was studied at Floyd Bennett Field, Brooklyn NY. The 579 ha site, originally salt marsh filled in to construct an airport, consists of mid-successional habitats such as grasslands, native shrub thickets, developing woodlands, and mixed stands dominated by giant reed (Phragmites australis). The site is now managed by the U.S. National Park Service for recreation and ecological restoration. Prior to this project, the site did not support populations of these species.

Eastern box and painted turtles were collected and released after data on size, weight, age, and sex were recorded. In 1990, 55 painted turtles were released into a 0.3 ha pond created in 1989. These individuals were monitored using funnel traps through the end of 1993. From 1987 through 1990, 335 box turtles were released into developing woodlands, most after 30 days in an acclimation pen. Fifty three individuals were fitted with radio-transmitters and monitored for up to seven years. Additional data were obtained through active search and the use of a Labrador retriever.

Recapture rates of _C_. _picta_ ranged from 87.8% to 97.7 % annually, indicating they remained at the release pond and had high survival. Growth varied by sex and age, and fecundity was estimated at 11.7 eggs/adult female/year. Rates for these parameters were comparable to similar non-repatriated populations.

Though individually variable, _T_. _carolina_ tended to disperse homeward after release. Of the 53 radio-tagged individuals, 13 (24.6%) left the site, 25 (47.2%) established home ranges, and 15 (28.3%) died before sufficient data were collected. Most individuals radio-tracked long term established home ranges within a kilometer of the release point. Some may disperse 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.

These generally positive results were mitigated by low rates of survival. Annualized survival of _T_. _carolina_ for five years post-release was 71%, with lowest survival in the first two years. Principal causes of "mortality" were dispersal from the site and pneumonia, both of which were greatest initially, plus winter kill, a random event. Annualized survival for the final three years was 84%. Patterns of growth, home range size, activity season, habitat use, annual reproductive output, and production of young were generally comparable to similar populations of _T_. _carolina_ not subject to repatriation.

These results, based on short to intermediate-term monitoring indicate that _C_. _picta_ may be easily repatriated, but that _T_. _carolina_ is more difficult. Assuming a circular shape, release sites for _T_. _carolina_ need to be at least 300 hectares of predominantly woody habitat in order to retain most individuals, and initial mortality rates may be relatively high. Data on behavioral and reproductive parameters suggest that a population is in the process of becoming established, but conclusions on long-term results will require follow-up assessment after another 20-30 years.

Acknowledgements

The work presented here was made possible only by the assistance, encouragement, and support of numerous people and institutions. The National Park Service provided principal funding and logistical support. I am especially grateful to Dr. John Tanacredi, whose support and encouragement was critical, as well as Gateway General Superintendents Robert MacIntosh and Kevin Buckley. Al Breisch provided the study's impetus. John Behler provided training in radio-telemetry and generously made available the resources of the Wildlife Conservation Society.

The City University of New York provided additional financial and facility support, but most importantly, the intellectual support needed to develop this project into its final form. I am extremely grateful to my advisory committee. Max K. Hecht served as my advisor and mentor. His guidance was critical in the development and maturation of my ideas, and the shaping of this project. Robert Madden shared his knowledge of homing and experiences radio-tracking box turtles, and both he and Leslie F. Marcus provided extensive and patient statistical advice. Carol Simon also provided her knowledge of homing and reptile field studies and Andrew Greller his understanding of the ecology of Floyd Bennett Field.

Implementing this project would not have been possible without the help of many people. I would like to acknowledge the important contributions of Peter Warney, Norm Soule, Allen Salzberg, Al Lindberg, Bill Holmstrom, and Frank Indiviglio in obtaining animals for repatriation. Many Gateway staff assisted in collecting monitoring data and provided companionship in the field. These include Peter Warney, Craig LeShack, Haley Ferraro, Tracy Crowningshield, Mike Risinit, and Jim McDougal, as well as Dave Taft, Rita Mullally, Nancy Corona, Don Riepe, Kevin McCready, Ann Scaglione, Carol Thompson, John Pryzmocki, Rick O'Neil, and Reno. Similarly, NPS volunteers Barry Smith, Nancy Chang, Diana Popp, and Lisa Couturier gave freely of their time and energies. Also, to all those visitors and citizens who took the time to call in with reports of tagged turtles, my many thanks.

Special thanks are due to Allen O'Connell for his help in obtaining "Gus", and of course, to "Gus" himself. His skills at retrieving box turtles (once all pheasants were flushed) helped to greatly expand my data. Thanks are also due to Rich Lent, for assistance with GIS and habitat analysis.

Ultimate thanks go to my wife, Mary Hake. Her support and supreme patience during the many years of this project were most critical to its success. I can only hope to give to her all that she has given to me over the years.

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Chapter 1. INTRODUCTION

Population declines and the conservation of turtles is a global issue commented on in recent years by numerous authors. It affects all turtle groups, whether grouped taxonomically or by habitat, and is due to a number of factors. Major factors in these declines include harvesting of eggs and adults for food, collection for the pet trade, accidental death from commercial fishing or road kills, and the loss or alteration of habitats (Bury 1979, 1982, Carr 1967, Diemer 1989, Klemens 1989, Stubbs and Swingland 1986).

Among the conservation strategies aimed at addressing these issues is repatriation, defined as "the intentional release of individuals of a species into an area formerly occupied by that species" (Reinert 1991). Dodd and Seigel (1991) note that while repatriation programs are increasing in popularity, serious questions have arisen about the theory behind and effectiveness of such programs. One question is whether repatriation programs actually result in establishing viable populations or merely serve to perpetuate an unjustified perception that such programs are successful, and thereby undermine efforts based on more certain methods such as habitat protection.

While instances of intentional or inadvertent repatriation can be found for many species among the Testudinidae, the gopher tortoise (Gopherus polyphemus) and the desert tortoise (G. agassizii) have the most detailed record. In an extensive review of gopher tortoise relocations, Diemer (1989) noted that previous studies had provided minimal or conflicting data regarding the fate of relocated animals. In a similar review of desert tortoises, Berry (1986) noted that relocated 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, and therefore did not indicate whether relocation was feasible. Thus these reviews support the contention of Dodd and Seigel (1991), that repatriation is an experimental technique requiring long term monitoring to determine if it is successful.

In addition to repatriation, restoration and rehabilitation of habitats altered by human activity is another conservation strategy of increasing popularity. While the goal of habitat restoration projects vary, they all attempt in varying degrees, to restore the site's original biota, or to manage the site to favor a particular species (e.g. a particular endangered species).

Monitoring of rehabilitated sites has shown that species composition of herpetofauna present varies depending on rehabilitation techniques, and that these differences are related to the presence or absence of key habitat elements for a particular species of herpetofauna (Nichols and Bamford 1985). For example, two reclaimed phosphate mine sites in Florida were used as donor sites for repatriated gopher tortoises. Based on two years of monitoring, higher site fidelity and shorter dispersal distances occurred at the site of higher habitat quality (Godley 1989). Thus while "natural" areas created by human activity (e.g. dredge spoils) or as a result of site "restoration" have potential for playing a role in species conservation efforts, this strategy also remains one which must be evaluated more critically, and from the perspective of meeting the needs of a particular species or group of species.

The eastern box turtle (Terrapene c. carolina) and painted turtle (Chrysemys picta) are both species that have previously been considered widespread and common (Conant and Collins 1991, Ernst and Barbour 1972). In recent years, however, population declines in T. carolina have been reported by Albright (1986) and DeGraaf and Rudis (1983) in New England, by Stickel (1978) in Maryland, Mount (1986) in Alabama, and Dodd (1992) in Florida. Urbanization, agriculture, logging and road construction (which fragment and eliminate Terrapene habitat), coupled with commercial over-collecting, in their cumulative effect pose a serious threat to the long term viability of Terrapene populations (Lieberman 1994). In the

New York Metropolitan Area, T.c. carolina has declined in Westchester County (immediately to the north of New York City) though populations are still surviving in patchwork habitats (Klemens 1989). In Nassau County (immediately to the east of NYC), it is considered endangered (Schlauch 1978). In Brooklyn (Kings County), native populations of eastern box turtle are extinct. While a range-wide decline of painted turtles has not been reported, in New York City this species has declined and only occurs in the relatively few ponds remaining in parks.

1.A. STATEMENT OF PROBLEM

As part of a larger program of herpetofaunal community restoration (Cook 1989), Eastern Box Turtles (T. c. carolina) and Painted Turtles (C. picta) were repatriated to Floyd Bennett Field, Brooklyn, NY. This 579 ha site is human-created, resulting from dredge spoil deposition and landfilling during the period from ca. 1928 through 1945. It presently contains grasslands, shrub thickets, developing woodlands, a freshwater pond, and wetlands composed of both native and alien species. The purpose of the repatriation program is to establish populations of these turtle species on this now-protected parcel of land. Floyd Bennett Field is within these species' historic range but, prior to the initiation of this program, there were no populations of eastern box turtle or painted turtle extant there. In addition to this formal program, throughout the range of T. carolina individuals, (e.g. those found crossing roads), are frequently repatriated by concerned humans to sites deemed "safer" (see Anonymous 1993). Thus numerous impromptu repatriations of *T. carolina* are also carried out in many parts of its range.

As with *G. polyphemus* and *G. agassizii*, existing data (e.g. Doroff and Keith 1990, Metcalf and Metcalf 1978, Nichols 1939, Schwartz and Schwartz 1974) are insufficient to determine the frequency of the various post-repatriation responses, and thereby assess the extent to which repatriation is a successful or "feasible" strategy. Data on the fate of repatriated individuals are needed to determine the outcome of these efforts, and aid in assessing the potential of repatriation as a conservation strategy for these two species.

In monitoring the fate of individuals repatriated in this program, questions along two general though interrelated themes arise. First, what is the behavior and ecology of the transplanted animals? To what extent do they remain at the point of release? For example, homing is well documented in both species (Cagle 1944, DeRosa and Taylor 1980, Gould 1957, 1959, Lemkau 1970, Madden 1975, Nichols 1939, Williams 1952) and repatriated individuals may not remain on the release site. There are however, many instances where displaced individuals, particularly those moved distances in excess of 5-10 km, remained at the release site or did not home (Cagle

1944, Doroff and Keith 1990, Emlen 1969, Gould 1957, 1959, Nichols 1939, Posey 1979, Schwartz and Schwartz 1974). Similarly, how far do repatriated individuals disperse? While their movements may not be oriented toward home, they can still be oriented, and result in the displaced individuals leaving the release site (Hall 1987). This may be an important factor in determining success, as well as in developing guidelines for minimum sizes of areas to be used for repatriation. The important question from the point of view of repatriation success or failure is not necessarily the extremes of these behaviors, but rather the frequency of the different responses (Berry 1986).

Beyond merely remaining at the release site, many other questions remain concerning repatriated turtles. To what extent will they establish home ranges and if so, what size? How stable are home ranges and activity centers over time? What are the patterns of survival, growth, habitat selection, fecundity, food utilization, hibernation, and activity period? How do these parameters for the repatriated population compare to natural populations?

The second theme concerns the human-created habitats and their suitability for supporting populations of eastern box turtles and painted turtles. In many respects these are the same questions already asked, but from the perspective of the habitat. Do these habitats provide the resources necessary for the survival and reproduction of the repatriated animals? How do patterns of habitat utilization at this site compare with studies of populations on natural habitats? How plastic are these species in utilizing human-created habitats?

Thirdly, questions arise as to potential differences between aquatic and terrestrial turtles in the ability to repatriate them and monitor the results of these efforts. For example, to what extent do differences in longevity, reproductive strategies, activity patterns, and habitat use influence the ability to successfully repatriate and monitor populations?

The research presented herein examines the hypothesis that eastern box turtles and painted turtles can be successfully repatriated to a human-created "natural" area. Griffith et al. (1989) define success as resulting in a self-sustaining population, with the converse being the extinction of the founder group. While criteria for determining success are definable in general terms, threshold values for various life history parameters that would indicate ultimate success or failure have yet to be developed. Moreover, such values would be species-specific, and probably site-specific as well.

As discussed by Dodd and Seigel (1991) and Burke (1991) evaluation of repatriations will require long term monitoring, probably in excess of 20 years in the case of tortoises. While such long term monitoring is necessary to determine ultimate outcome, shorter term monitoring provides, in a qualified sense, an indication of a repatriation's likelihood of success or failure. This in turn may aid in conservation decisions that can not be deferred until the long term results are available.

It is my contention that in an idealized repatriation (with donor and release site being equal in habitat quality), one indicator of success would be that the behavior and ecology of repatriated individuals at the release site should parallel that at the donor site. Lacking this population-specific data, data from other populations can form a basis for comparisons, taking into account all real world differences such as climate, habitat, population density, and food availability.

While it is difficult to determine at what point in time a repatriation is successful, there is an idealized sequence of events which must occur if success is to result. Individuals must remain at the release site, survive, feed, grow, encounter each other for reproductive purposes, and produce offspring, which in turn survive, etc. Thus measuring these parameters for a repatriated population, and comparing them with "norms" for the species, can provide indices by which success can be evaluated.

Chapter 2. MATERIALS AND METHODS

2. A. Study Site

The study was conducted at Floyd Bennett Field, a 579 ha site in Brooklyn, NY managed by the National Park Service as part of Gateway National Recreation Area (Figure 1). The site, originally salt marsh filled in to construct an airfield, is composed primarily of early successional-stage habitats, including; mixed grasslands; thickets dominated by bayberry (*Myrica pennsylvanica*), blackberry (*Rubus* sp.), and sumacs (*Rhus* sp.); pioneering woodlands composed of black cherry (*Prunus serotina*), 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; and stands dominated by giant reed (*Phragmites australis*) (Figures 2 and 3). While a 1984 vegetation analysis found *Phragmites* to be the single most dominant cover type (Lent and Litwin 1989), recent analysis, based on 1992 conditions indicate that woody plant succession is beginning to reduce the dominance of this covertype (Figure 2). The relatively large vegetated tracts are separated by paved runways ranging from 33 to 100 m wide (Figures 2 and 3).

2.B. Turtle Repatriation and Field Data

Eastern box turtles and painted turtles were collected from a number of sites in Nassau and Suffolk Counties, NY and repatriated to Floyd Bennett Field. Prior to release, all turtles were marked for individual identification by shell notching (Cagle 1939), and sex, weight, carapace length, carapace width, age (when possible), and reproductive condition recorded.

2.B.a. Painted Turtles (Chrysemys picta)

In 1990, 55 adult and sub-adult painted turtles were collected on Long Island, NY and released into Return-A-Gift Pond (RAG), a 0.3 ha. pond created by excavation of a giant reed marsh in 1989 (Figure 3). Distance repatriated ranged from 27 to 129 km (mean=72.7, standard deviation (SD)=28.2). Twenty two were released directly into the pond. The remaining individuals were placed in a pen in the pond, to be held for 10 days, and then released. Of these 33 individuals, 12 escaped into the pond prior to being formally released.

The fate of released and escaped individuals was monitored primarily by trapping with funnel traps, and to a very minor extent by dip netting and hand capture. Trapping effort during the period 1990 through 1993 totalled 1736 trapdays (Table 1a). Each trap placed in the morning and checked on the following morning constituted a trapday. At each recapture, weight, carapace length and width were measured, and females palped for eggs. Beginning in September 1991, plastron length was also recorded. In addition to palping, females were X-rayed (Gibbons and Greene 1979) on 10 June 10 1992, 28 May

1993, 10 June 10 1993, and 25 June 1993 to determine the presence and number of eggs. Palping was generally a reliable way to determine presence of eggs, though, unlike X-rays, it provides no data on clutch size. In 1993, I was able to palp 95% (35/37) of all individuals attempted. Of those successful attempts, the rate of false positives (palping positive but yielding a negative X-ray) was 4%, whereas that of false negatives was 10%.

2.B.b. Eastern Box Turtles (*Terrapene c. carolina*)

During the period 1987 through 1990, 335 eastern box turtles were repatriated to Floyd Bennett Field (Table 2). All were marked and, with some exceptions, weight, carapace length, and carapace width measured. Plastic tags (13 mm dia.) imprinted with an identification number, plus a message and phone number, were attached to the carapace with epoxy glue. Annuli were counted on young individuals, but the majority were adults with greater than 15 annuli, and thus beyond the age for which annuli counts are reliable. With the exception of 53 individuals equipped with radio transmitters (discussed below), most individuals were held in a pen at the release site for ca. 30 days prior to release. All were released at one of two sites, with the vast majority released at a primary release site (Figure 3).

During the period 1987 through 1991, recaptures of animals without radios were made incidental to radio-tracking, in active search, and through incidental encounters by other park employees and visitors. At each recapture, data on location, general activity, general habitat, general weather, and weight were recorded. In 1992 and 1993, data on environmental and cloacal temperatures, vegetation height, and carapace length and width were also recorded. From 1993 through 1995 a trained Labrador retriever (Schwartz and Schwartz 1974) was used to concentrate effort on recapturing as many individuals as possible, thereby minimizing the percentage of individuals whose fate is unknown, and to generate growth data.

From 1988 through 1990, 53 individuals (out of the 335 total) were equipped with radio transmitters, released at the primary release site, and followed. The histories of these animals were diverse. Some were collected from the wild while others were collected at sites slated for construction or while crossing highways. Many were kept as pets for varying periods of time before release. The extent to which these different histories might influence post-release movements is unknown, but may be significant. Nowhere in the literature are there references to the post-release behavior of individuals kept for periods of time prior to release.

In addition, handling at the release site could influence post-release behavior. For example, holding animals in pens _in situ_ at the release site might result in an acclimation to the release site, and a lessening of potential homing response. Such penning has been used with mixed results in gopher tortoise repatriation programs (Stout et al. 1989, Godley 1989).

As a test of the influence of these variations in handling history, box turtles released with radio transmitters were divided into four categories that reflect differences in handling prior to, as well as after arrival at the release site. Each category consisted of 12 to 15 individuals. _Wild_ individuals were those taken from the wild and brought to the release site within seven days. Mean time between capture and arrival at the release site was 4.3 days (range one to seven days, SD=2.1).

Pets were individuals held in captivity, off-site, for a minimum of thirty days. Mean time held in captivity prior to arrival at the release site was 87.8 days (range 30 to 139 days, SD=29.5). Since "pets" hibernated in outdoor pens, all calculations of time in captivity are based on activity season days or "active days", not calendar days. Turtles of both categories were released immediately at the primary release site (_0_ days) or held in an acclimation pen at the primary release site for 15 days prior to release. Box turtles released without radio transmitters were held in the acclimation pen for ca. 30 days prior to release.

The two stage transmitters with whip antennas operated in the 164 Mhz band, and were mounted by gluing with epoxy to the turtle's carapace. The transmitter was attached directly above the posterior marginals and the antenna directed anteriorly, attached to the marginals. A model made by L.L. Electronics (Mahomet, IL) was used 75% of the time. The radio package (transmitter plus epoxy) weighed ca. 20 grams, which represented 2.5% to 9.0% (mean 4.2%) of the turtle's body weight. A second model, made by ATS (Ypsilanti,MN) was used the remaining 25% of the time, and had a package weight of 23 gm, representing 2.8% to 5.2% (Mean 4.1%) of body weight.

Turtles were recaptured using an AVM LA-12 radio receiver (164 Mhz) and data on location, general weather conditions, macro and micro-habitat, heading, weight, and other behaviors recorded. Turtles were recaptured daily for the first three days following release, then weekly and, as elapsed time from release increased, the frequency of recapture decreased. However, individuals showing rapid or otherwise "unusual" movements were followed more closely than slower or more sedentary individuals. The intensity of long term monitoring varies, with intervals between recaptures ranging from ca. one to three weeks. Problems with radio failures were initially common, and the length of monitoring period ranges from a few days to over five years.

During the 1992 and 1993 activity season, radio-tagged box turtles were relocated ca. weekly. In addition to location and weight, data collected at each relocation included surface, air, and cloacal temperature, litter depth, relative humidity, % soil moisture, % carapace exposed, % shade, and vegetation height. When a turtle was buried, as in a form or hibernaculum, data on depth and temperature at carapace and plastron level was measured. Carapace length and width were measured whenever radios were changed. In addition to palping for eggs, all females were X-rayed on 30 June 1992, 10 June 1993 and 25 June 1993. Weekly monitoring continued until turtles entered hibernation in the fall of 1993. All radio transmitters were removed on 15 December 1993. Limited field work was conducted in 1994 and 1995 to provide additional data on growth, survival, and records of progeny (Table 1b).

2.B.c. DATA ANALYSIS

Field data were analyzed as follows, with the significance level for all statistical tests $p<0.05$;

Dispersal Direction of Box Turtles - Randomness of dispersal and homing was based upon analysis of vanishing bearings

(Batschelet 1981) of radio-tagged individuals. Madden (1975) found that some displaced animals remained within 50 m of the release site for several days, wandering randomly before showing homeward movement. Thus vanishing bearings were calculated as the bearing between the release point and the point at which the box turtles crossed imaginary circles 100 m and 200 m in radius centered on the release point. The Rayleigh test (Batschelet 1981) was used to test if vanishing bearings are significantly oriented. In addition, since the homeward direction is known, the 'V' test was used to test if the vanishing bearings are clustered around the homeward bearings, and thus differ from randomness (Batschelet 1981). For this analysis, vanishing bearings were transformed to reflect a standardized homeward bearing of 0 degrees magnetic.

Distance Dispersed - Locality data were used to calculate straight line distance from release point as a function of time since release. It was anticipated that all individuals would initially show a positive relationship. For individuals exhibiting uni-directional movements this relationship would persist, whereas, if individuals establish home ranges, the distance-time relationship would level off. Maximum distance from release site, and the elapsed, active season time taken to reach this maximum distance were determined for each individual released with a radio. From these individual data, analysis of frequency distributions was conducted to determine the minimum sized parcel required to contain different percentiles of the repatriated population, and the time taken by these individuals to disperse.

Home Range Size and Stability- Home ranges of radio-tagged box turtles were calculated using the bivariate normal (95% ellipse) method (Jennrich and Turner 1969), and the harmonic means method (Dixon and Chapman 1980). Madden (1975) points out that the bivariate normal has the advantage of being independent of sample size, but is insensitive to cases where activity has a number of centers due to patchy habitat. Whereas both the bivariate normal and harmonic means methods base home range estimates as probabilities and allow calculation of activity centers or centers of gravity, the harmonic means method is sensitive to heterogeneity of habitat and is capable of identifying more than one center of activity (Dixon and Chapman 1980). While the harmonic means method is likely a more realistic representation of the animals's use of space, and thus more desirable, comparison with other studies was based on the 95% bivariate normal method. For individuals with sufficient multi-year data (a minimum of 10 points per year) stability of geographic center of home range was analyzed .

Habitat Selection - Aerial photographs (scale 1:2400, flown 4/6/92) were used to map major habitats at Floyd Bennett

Field, using the vegetation types of Lent and Litwin (1989). Data on habitat selected by T. carolina, obtained by extracting habitat data for each location recorded on an animal's home range, was tabulated, in total and by season. Analysis compared frequency of occurrence of T. carolina in each habitat with habitat frequency (% of available area) to determine if habitat use is random.

Growth - For both T. carolina and C. picta data on growth were used as an index of repatriation success and habitat suitability. Changes were analyzed, taking into account factors such as age, sex, and elapsed time. While difficult to state in terms of absolutes, it seemed reasonable to expect that for a repatriation to be successful, repatriated individuals would show patterns of growth that compared favorably with individuals in natural populations. While it is probably not possible to state threshold values for what constitute successful versus unsuccessful rates of growth, data demonstrating relatively little or no growth (in size/age classes expected to grow), would suggest that repatriation is not likely to be successful.

Fecundity Rate and Clutch Size - Data from X-radiography of females provided estimates of fecundity rates, clutch size, and annual reproductive output. These data were compared with natural populations. In addition to their demographic value, since the kinds and amount of food available influence reproductive output by affecting energy reserves available for reproduction (Moll 1979), these data also provide an index of habitat quality.

Survival - Data from trapping, radio-telemetry, and capture by hand and dog were used to estimate survival of the two species over the course of this study. These were analyzed to determine if survival differed as a result of age, sex, or treatment prior to release and compared with published data from other populations. In addition, when possible, sources of mortality were identified.

Chapter 3. RESULTS

3.A. Painted Turtle

3.A.a. Survival

Survival of Long Island, NY C. picta repatriated to Return-A-Gift Pond on Floyd Bennett Field, Brooklyn in 1990 was calculated as percentage of individuals, grouped by ages, sex, and as a complete cohort, surviving given intervals of time. Annual survival rates for each group were calculated for the periods 1990 to 1991, 1991 to 1992, and 1992 to 1993, as well as for the entire period of the study, 1990 to 1993.

Annual survival was generally high, though variable between groups and time periods (Table 3). For the entire cohort (all ages and sexes combined) annual survival rates were 89.1%, 87.8%, and 97.7% for the periods 1990 to 1991, 1991 to 1992, and 1992 to 1993 respectively. For these same time intervals, annual survival of adults was 86.7%, 84.6%, and 100.0%, and similarly for juveniles, 100.0%, 100.0%, and 90.0%. Survival of the entire cohort, for the period 1990 through 1993 was 76.4%. Adult survival during this three year period was 73.3%, whereas juvenile survival was 90.0%.

For individuals released directly into the pond, survival from 1990 through 1993 was 81.8% as opposed to 83.3% for animals that escaped from the acclimation pen and 67% for animals held in the pen for 10 days prior to release (Table 3).

Chrysemys survival was analyzed in a number of ways. Differences in numbers of individuals surviving from 1990 to 1993 due to age, sex, and pen treatment were analyzed both as single factor analyses using the chi-square test, and as multi-factor models using logistic regression procedures (SAS Institute 1990).

Based on single factor chi-square tests, there were no significant differences in survival due to age, sex, or pen treatment (Table 4). Since all juveniles were females, age effects were only tested among the females. The effect of holding for 10 days prior to release was further tested by comparing animals held for the full ten days against those not (ie. those released immediately and those that escaped from the pen). Survival from 1990 to 1993 did not differ between these two groups.

Stepwise logistic regression was also used to analyze the effects of age, sex, and pen treatment on the numbers of individuals surviving from 1990 to 1993. No significant effects due to any of these three variables were found (Likelihood ratio chi-square=3.34, df=1, p=0.07).

Effects of sex, age, and treatment on survival were also analyzed based on survival times of individuals (ie. number of years survived beyond 1990) using proportional hazards regression and SAS proc LIFEREG (SAS Institute 1990). Models of main effects, with and without two-way interactions were tested. There were no significant differences in the distribution of survival times attributable to age, sex, treatment, or their interactions (Table 4).

LIFEREG fits a parametric model to failure or survival time data. Due to the presence of zero values for some of the observed failure times, the NOLOG option was used, which fits an extreme value distribution to the raw data. Based on this test, there were no significant differences in the distribution of survival times attributable to age, sex, or treatment (Table 4).

In all instances, survival calculations were based on live recaptures (ie. individuals known to be alive at a given point in time). During any given trapping period, trapping was continued far beyond the point where new captures for that trapping period were recorded. In no instances did any individuals skip capture in a year, ie. no individuals were recaptured in a year subsequent to one in which they were not. Thus these data can be considered an accurate representation of the entire population present in the pond at a given point in time.

3.A.b. Growth

Growth of C. picta was measured as growth in plastron length in millimeters (mm). Plastron growth was highly variable (both in actual increments and percent growth) and reflected differences due to initial size, sex, individual and annual variation (Figures 4,5,6). Mean growth in males and females, by size group and year, as well as for the entire three growth year period are presented in Tables 5 and 6. Growth was greatest in the smallest size classes, with larger size classes within each sex showing little or no growth. Percent growth within any given size class was greatest in the 1991 growth season and least in 1993. Total rainfall amount during the growing season (May through August on Long Island (Zweifel 1989)) were similar in 1991 and 1992, 41.07 and 43.48 cm respectively, whereas in 1993 it was only 19.28 cm (Table 7).

3.A.c. Reproductive Output

Data on reproductive output are based on X-rays of adult females. Any female with a plastron length greater than 110 mm was considered adult (Zweifel 1989). In 1992, 29% of the females checked were gravid and mean clutch size was 7.0 (Table 8). These data, however, were based on only one sampling date (10 June 1992) and are inadequate.

Results from 1993 are based on three sampling dates distributed across the nesting season (28 May, 10 June, and 25

June) and provide more complete data on the number of individuals producing clutches, as well as clutch size and number. In 1993, 75% (15/20) of the adult females checked were gravid. Of these 15, seven produced only one clutch, and the remaining eight produced two clutches (Table 8). Mean clutch size for all 23 clutches recorded in 1993 was 7.5. Mean size of the first clutch (all seven individuals that produced only one clutch, plus the first clutch of those eight individuals that produced two clutches) was 8.1, and mean size of the second clutch was 6.4 (Table 9). In the eight individuals that double clutched, the mean of the first clutch (8.6) was significantly larger than the mean of the second (6.4) ($p=0.03$, paired t-test, two-tailed).

Relationships between plastron length of females and reproductive output in C. picta were analyzed using 1993 data. Mean plastron length of individuals producing zero, one, and two clutches differed significantly (one way anova $F=8.81$, $df=2,117$, $p=0.002$), with mean plastron length greatest in the group that doubled clutched and least in the group that produced no clutches (Table 10).

While these data suggest a positive relationship between plastron length and clutch frequency in 1993, most of the individuals that produced zero clutches were small, presumed to be adults on the basis of their size. This technique for determining sexual maturity is only approximate. That these smaller individuals did not produce any eggs suggests that they were not yet mature.

Based only on data from individuals that produced at least one clutch of eggs, those producing two clutches were larger than those producing one clutch (Table 10), but the difference in plastron length was not significant (one way anova, F=3.95, df=1,13, p=0.68). There was however, a significant correlation between total reproductive output and plastron length (Spearman Correlation Coefficient=0.62, p-0.01), indicating that annual egg production tended to increase with size (Figure 7).

3.B. Box Turtle

3.B.a. ACTIVITY SEASON

The active season for T. carolina on Floyd Bennett Field was determined through year-round monitoring of radio-tagged individuals. For these individuals, the beginning and ending of the activity season were estimated by "bracketing" (Claussen et al. 1991). In the spring, the mid-point between the last date recorded in hibernation and the first date recorded out of hibernation was used to estimate the beginning of each individual's activity season (spring emergence). A similar process was used to estimate the date activity ended and hibernation began. Based on the sample of individuals being monitored in a given year, estimates of the mean dates of spring emergence and fall hibernation, and mean length of activity season, were calculated for each year. For the entire study period (1988 through 1993), the mean activity season extended from 21 April to 24 October, and lasted 185 days (Table 11).

All subsequent analyses with a temporal component (ie. number of elapsed active season or activity days) are based on these data as follows. When individual-specific data on the dates of activity were available, these were used. If not available, then year and season-specific means were used. For example, if a turtle had been missing due to radio failure and actual dates of hibernation and emergence unknown, mean values for the appropriate fall and spring would be used. For the few individuals recaptured in 1994, the overall mean date of spring emergence 21-April was used.

3.B.b. ACTIVITY

Upon each relocation of radio-tagged individuals, the animal's activity was recorded. A total of 2,097 active season records were obtained from all the radio-tagged *Terrapene*, ie. the 53 individuals initially released with radios, plus the 21 individuals that had radios subsequently mounted in 1992 or 1993. The most frequently observed activities were various forms of resting or stationary attitudes, accounting for 84.3%

of all observations (Table 12). Other observed activities included walking, basking, soaking, swimming, feeding, drinking, and defecating.

A total of 34 observations involved close proximity (less than 0.5 m) between individuals or actual interactions. There were two observations of courtship and eight of matings. In the remaining 24, there was no interaction observed other than close physical association (Table 12).

3.B.c. DISPERSAL

Dispersal from the release site was looked at in terms of direction, speed, and ultimate distance.

3.B.c.1. Direction

The mean homeward direction for all turtles was 82.1 degrees magnetic (vector length r=0.982). Mean homeward direction for each of the four treatment groups ranged from 77.7 to 85.6 degrees (Table 13). The high values of vector length (r) (maximum possible is 1.0) indicate the close clustering of individual bearings around the mean. The Mardia-Watson-Wheeler Test, a determination of whether two or more samples differ from each other (Batschelet 1981), shows that when analyzed as a multi-group test between the four treatment groups based on origin and number of days in holding pen (ie. pet0, pet15, wild0, and wild15), the between group home bearings are not significantly different from each other (chi-square=9.2, df=6, P=0.16). Thus each of the four treatment groups have the same, essentially eastward homeward direction. This is due to the fact that all animals were collected from Nassau and Suffolk counties on Long Island. These counties lie east to east-northeast of Brooklyn, and Long Island is a long, narrow island oriented east-west.

Mean distance repatriated was 70.2 km (SD=22.9) and ranged from 32.2 to 131.3 km. Mean distance repatriated 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 repatriated (one way ANOVA F 3,48=3.32, p=0.03). Tukey's studentized range test indicated there were two groupings. The first consisted of pet15, pet0, and wild15, and the second consisted of pet0, wild0, and wild15.

Dispersal direction was calculated as the vanishing bearing, the bearing from the release point to the vanishing point. In this study, the "vanishing point" was the point where turtles crossed the imaginary circular lines of 100 m and 200 m radius drawn around the release point.

Mean dispersal direction for all individuals combined, measured as the 100 m and 200 m vanishing bearing was 49.2 degrees magnetic (r=0.274) and 66.0 (r=0.244) respectively.

Differences between the 100 m and 200 m vanishing bearings were not significant (Mardia-Watson-Wheeler chi-square=0.5, df=2, p>0.61), suggesting that either radius is adequate for determining vanishing bearings in Terrapene, and that results of analysis based on the two different radii will be duplicative.

Mean vanishing bearings for each of the four treatment groups ranged from roughly north-northwest to easterly (Table 14). Results of the Mardia-Watson-Wheeler test show that when analyzed as a multi-group test (ie. pet0, pet15, wild0, and wild15), the between group vanishing bearings can be considered as coming from parent populations that are not significantly different. However, two-sample comparisons indicate inter-group differences in 100 m vanishing bearings between pet15 voice pet0, and pet15 voice wild0. At 200 m, the only significant differences were between pet15 and wild 0 (Table 14).

While the Mardia-Watson-Wheeler Test tests for differences between sample groups, it does not address the question of randomness versus directedness in the vanishing bearings.

The modified Rayleigh or V-test is used to test the null hypothesis of randomness when a preferred direction (e.g. home) is expected. It incorporates knowledge of the presumed direction, testing whether the observed bearings have a tendency to cluster around the expected, and thus whether the distribution differs significantly from random (Batschelet 1981).

In performing the V-test, all actual vanishing bearings were transformed to provide for a standardized home bearing of zero degrees. For each individual, the home bearing was set to zero degrees. The actual vanishing bearing was then transformed to a bearing that deviated from zero degrees in the exact same manner (ie. magnitude and direction) as the actual vanishing bearing deviated from the actual home bearing. For example, if the actual home bearing was 40 degrees and the actual vanishing bearing 50 degrees, then the transformed vanishing bearing for this individual is 10 degrees. Had the actual vanishing bearing been 20 degrees, the transformed value would be 340 degrees. With transformed bearings, zero (or 360) is the homeward direction.

Using transformed bearings, results of the Mardia-Watson-Wheeler test, show that when analyzed as a multi-sample test (ie. pet0, pet15, wild0, and wild15), the between group vanishing bearings can be considered as coming from parent populations that are not significantly different. However, two-sample comparisons indicate inter-group differences in 100 m vanishing bearings between pet15 v. pet0, pet15 v. wild0, and all pen0 v. all pen15. At 200 m, there are significant intergroup differences between pet15 v. wild0 and all pet v. all wild (Table 15).

Results of the V-test performed on both 100 m and 200 m transformed vanishing bearings indicate that for all individuals pooled together, dispersal was significantly clustered around the homeward bearing (Table 15). When classified by origin, pets were significantly clustered whereas dispersal of wild individuals did not differ from random. When classified by treatment, individuals held in the pen for 15 days were significantly clustered, whereas individuals released immediately (pen 0) dispersed randomly. When broken down into the four treatment groups, the dispersal of pet0, wild0, and wild15 turtles was random and not directed. However, the dispersal of pet15 turtles was highly directed, and had a highly positive home component. Because dispersal of pet15 turtles was highly clustered (r=0.85) and had a large home component (hc=0.74), any larger group that contained these 11 individuals also showed significant differences from randomness.

Though the V test indicates that the dispersal direction of all individuals combined, pets, all animals held in pen 15 days, and pet15's is not random, and therefore directed, this is not a test of homing. Tests of homing require calculation of a confidence interval for the mean bearing and a determination if the home bearing lies within that confidence interval (Batschelet 1981).

If the home bearing (0 or 360 degrees) in the case of the transformed vanishing bearings) is within the 95% confidence interval of the mean, then the hypothesis of homing can not be rejected. Based on analysis of 100 m and 200 m vanishing bearings, all individuals, all animals held in the pen 15 days, and all pets homed. However, when each of the four treatment groups was analyzed individually, only the pet15's homed, and then, only when based on 200 m vanishing bearings (Table 16).

3.B.c.2. Speed of Dispersal

Speed of initial dispersal was measured as the elapsed active season time taken to reach the 100 m and 200 m radius (time100 and time200, respectively). The presence of animals that did not cross a given radius due to death, radio failure, or simply not moving that far, lead to the use of failure time analysis, ie. proportional hazards regression and SAS procedure PROC LIFETEST (SAS Institute 1990). In these analyses, "failure" equates to reaching a given radius, failure time is time100 and time200, and animals that did not cross a given radius are "censored" observations.

The time taken by individual turtles to reach the 100 m radius ranged from 0.3 to 460.0 days. For all individuals pooled together, mean time100 was 73.6 days. For the four groups time100 ranged from 24.3 to 85.4 days for wild0 and pet0 respectively. For time200, individuals ranged from 2.0 to 986.0 days, and the pooled mean was 116.9 days. Group means ranged from 29.9 to 125.7 days for wild0 and pet0 respectively. For both time100 and time200, the distribution is highly skewed towards the low end of the range, with only a relatively few high values (Figures 8 and 9). Based on mean and quantile values for the four groups, wild0 turtles were the most consistently rapid dispersers from the release site. However the differences between groups for time100 or time200 are not significant at the p=0.05 level (Table 17).

Mean and quantile values of time100 and time200 were calculated for pets v. wild and animals held in pen 0 v. 15 days. These show that wild turtles tended to reach the 100 m and 200 m radii faster than "pets". At the 100 m radius this difference was not significant, but at the 200 m radius it was (Table 17). The were no significant differences in time 100 or time 200 due to spending time in the holding pen (Table 17).

In addition to comparisons of dispersal speed between the four treatment groups, the effect of origin (wild v. pet) and time in holding pen (0 v. 15 days) was analyzed using proportional hazards regression. The analytical model considered these two sources of variation, plus their interaction. There were no significant differences in time100 or time200 due to origin or time in holding pen. For time 100, model likelihood ratio chi-square=0.68, df=3, p=0.88. For time200, model likelihood ratio chi-square=2.24, df=3. p=0.52.

3.B.c.3. Distance

The question of distance dispersed from release point, and its relationship to elapsed time was analyzed by plotting straight line distance from release point against elapsed active season time. Elapsed active season time is the number of activity season days that have elapsed since a given individual's release. For each Terrapene released with a radio transmitter, a series of points representing the animal's location at specific points in elapsed time were chosen, and straight line distance from the release point calculated. In reality, due to individual differences in the relocation schedule and activity season, the exact number of elapsed days to relocation points vary between individuals. To facilitate comparison, a series of standardized elapsed active time values or points in time were chosen. Time intervals between points were initially one day, then two days, and increased with time to one week, two weeks, and in the long term, to four weeks. The points in time for which distance values were calculated are shown as "ActvTime" in tables 18, 19, 20, and 21. For each individual, the date (and the turtle's location on that date) that represented the point in time closest to the standardized value was chosen.

Blank spaces in the columns of tables 18 through 21 indicate there are no data on an animal's location at that particular point in elapsed time. As can be seen in these tables, the duration of coverage varies between individuals. This is the result of radio failure, death, and in some cases (e.g. T020, T334, and T512), the animals probably left the study area and were not relocated subsequently. Gaps in an animal's data resulted when an animal was temporarily lost track of (usually due to radio failure) and then subsequently relocated and outfitted with a new radio.

As would be generally expected, straight line distance from the release point initially increased with time. Eventually, in most cases, increase in straight-line distance slowed down, reached a maximum and levelled off, relatively. However, there was considerable variation between individuals in the relationship between distance dispersed and elapsed active time (Figures 10, 11, 12, 13). Some individuals, e.g. T323 (Figure 10), dispersed relatively far and rapidly, reaching its maximum straight line distance of 912 m in 112 activity days. T512 also dispersed rapidly, reaching a point 1020 m from the release site after 84 activity days. It disappeared at the water's edge. Others also dispersed relatively far from the release point but took longer to reach their maximum distance. For example, T356 (Figure 10) ultimately attained a straight line distance from release in excess of 800 m, but did not reach this distance until after 672 activity days.

Most individuals for which long term data are available dispersed lesser distances than in the above examples, and took intermediate amounts of time to reach maximum distance (MaxDist) from the release site. Of the 52 Terrapene released with radios, 20 lack data beyond one full year's worth of activity (185 activity days). Data from these can not be considered meaningful for determining how far turtles dispersed from the release point. The remaining 32 turtles, their maximum distance from the release site, and the time to reach this maximum are presented in table 22. For these individuals, the maximum distance varied by an order of magnitude (from 113 to 1295 m), with a mean of 507 m (SD=343, median=370). The majority (60%) of individuals attained a maximum distance of less than 500 m from the release site, and only 10% went beyond 1000 m (Figure 14). The time taken to reach maximum distance was also extremely variable, ranging from 21 to 1036 activity days (Table 22), with a mean of 326 days (SD=279, median=238). Similar to maximum distance, the time to reach maximum distance shows a left-skewed distribution where the majority of individuals reached their maximum distance in a relatively short period (less than 300 activity days), and a few individuals took several years (Figure 15).

The data from Table 22 suggest a positive relationship between maximum distance and the time taken to reach that maximum. If such a relationship exists, these data may not be a reliable indicator of how far animals ultimately disperse from the release point. Linear regression showed a significant relationship between maximum distance and the time to reach maximum distance ($r=0.41$, $p=0.02$). This significant relationship, however, may be the result of bias in the data. For many of these turtles, the data are still relatively short term. Of the 32 turtles with data beyond one activity year, the data for 13 of them does not extend to two activity years. These animals might still be in the process of dispersing and had not really reached their maximum distance before they died or disappeared. For two of the longest term and longest distance sets of data (T343 and T365), the turtles had been missing for a few years prior to their relocation at points relatively far from the release site, as well as their last known location. These individuals may have actually reached these distances in less time than the recorded data indicate.

A total of 19 individuals have data that extend beyond two activity years in time (Table 23). Linear regression of these data found no significant relationship between maximum distance and the time taken to reach that maximum (TimeToMax) ($r=0.40$, $p=0.09$). Thus this set of data represents a less biased sample for analyzing how far the Terrapene dispersed and the time taken to attain maximum distance.

For these 19 individuals, the maximum distance dispersed 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% of these Terrapene attained a maximum distance from release point of less than 500 m, 60% within 700 m, 80% within 1000 m, and 100% within 1,300 m (Figure 16). The time taken to reach maximum distance ranged from 21 to 1036 days, with a mean of 430 activity days (SD=319 and median=392). These data were also left-skewed, with 50% of the individuals reaching their maximum distance within 400 activity days (Figure 17).

3.B.d. Growth

Growth in T. c. carolina was calculated using carapace length in individuals measured at initial release and when recaptured in subsequent years. These include individuals with and without radios. Since recapture patterns varied between individuals, size data available for analysis generally consist of only a few measurements per individual, made at time intervals that range from one to six years. These data were simplified to two measurements (initial and final carapace length), and the time interval, in years, between the measurements.

Growth was calculated for each individual as the average annual percent growth rate using linear analysis similar to Stickel and Bunck (1989). In the present study, however, time in years rather than age was used as the independent variable in the relationship "natural log (Carapace Length)=slope*time + intercept". For each individual, the average annual percent growth rate was calculated as the slope of the line formed by applying the above formula to its data on size and time interval.

Since growth rates vary as a function of age (Stickel and Bunck 1989, others), Terrapene were grouped into age classes that combine the age class criteria of Stickel (1978) and Schwartz and Schwartz (1984). Four age classes were identified:

Class 1) Immature, less than 10 annuli present;

Class 2) Young adult, sexually mature, up to 18 annuli present;

Class 3) Middle-aged adult, greater than 18 annuli, carapace not smooth; and

Class 4) Old adult, carapace smooth.

Using these four age classes, and the average annual growth rates of each individual, average growth rates by age class and sex were calculated.

Average annual percent growth in carapace length was variable between and within age groups, with growth greatest in the immature (age class 1), intermediate in the young adult (age class 2), and least in the adults (age class 3 and 4) (Table 24, Figures 18-23). Results of two way General Linear Model (GLM) analysis of age class, sex, and interactions, indicate that age is the only significant source of variation (Table 25). Mean growth in age class 2 differed significantly from age classes 3 and 4, whereas there were no significant differences between age class 3 and 4 (Tukey's Studentized Range Test). Within age classes 1 and 2, but not 3 and 4, there was a significant inverse relationship between growth rate and initial size, indicating that smaller individuals tended to have greater growth rates (Table 26).

3.B.e. Survival and Mortality

Survival rates of repatriated Terrapene were calculated as the numbers and percentages of individuals known to be alive, dead, or status unknown over the course of time since release. Since winter kill is a major mortality factor in Terrapene (Metcalf and Metcalf 1979, Schwartz and Schwartz 1974), calculations of survival rate are based on the number of individuals known to survive through the winter from one activity season to the next. Calculation of survival and mortality is based on numbers of individuals known to be alive, dead, or status unknown as of the beginning of the spring activity season. Individuals classified as unknown may have left the site, or may be still be present, either dead or alive. Thus both survival and mortality represent minimums, and are conservative estimates.

The general pattern of survival is one of relatively low survival during the first year or two following release, with increasing rates of survival in subsequent years (Figure 24). This pattern is seen in percent survival of all Terrapene (both with and without radios) released in a given year (ie. 1987, 1988, 1989, and 1990), expressed as a percentage of the original cohort (Figures 25-28). A similar pattern is also seen when all cohorts are combined and the time element is expressed as "springs since release year" (Figure 29). Note however, that due to the staggered release of individuals over a four year period, sample sizes used to calculate percentages vary between outyears. Sample size for the first three springs since release year (sp1, sp2, sp3) is 335, whereas sp4=282, sp5=184, and sp6=62.

Year-specific percent annual survival varied between and within release year cohorts. The lowest was 27% survival by the 1989 cohort in the period from 1989 to 1990. The highest, 93%, was also for the 1989 cohort, from 1991 to 1992 (Figure 24). While these data illustrate the patterns of variation in percent annual survival, their utility is diminished by the relatively high number of individuals whose fate is unknown. A sub-set of these data, consisting only of radio-tagged individuals has a lower rate of "unknown", and correspondingly higher rates of individuals known to be alive or dead. Further calculation of survival rates was conducted on these data.

Radio-tagged Terrapene also experienced their lowest rates of survival in the fist year or two following release, with survival then increasing. In all cases, survival was lowest during the second yearly interval after release (Figure 30). For the cohort of 32 radio-tagged individuals released in 1988 (Figure 31), annual survival was 63%, 60%, 92%, 82% and 89% for the inter-year periods 1988-89, 1989-90, 1990-91, 1991-92, 1992-93 respectively. The 1989 and 1990 cohorts are similar, but are based on small samples.

Data from all three release-year cohorts can be combined to estimate survival in two ways. The first combines all individuals and expresses the time element as "springs since release year". In this approach, survival is looked at in relation to when an animal was released, rather than relative to specific calendar years (Figure 32). Survival to the first spring following release was 70%, with subsequent annual percent survival rates for the next four years 57%, 86%, 79%, and 89% respectively. The weighted average annual survival for these five years following release was 71%.

Survival was also calculated for specific calendar years, based on the individuals present at that point in time, regardless of when they were released. In this approach, animals released in a given year are combined with survivors from previous year(s) to determine the rate of survival to the next year. Percent annual survival ranged from a low of 63% from 1988 to 1989 to a high of 82% from 1992 to 1993 (Figure 33). The weighted average annual survival during this five year period was 71%.

Inter-year variation in survival was analyzed for the 1988 cohort, and the two forms of multi-cohort groupings. For all cohorts grouped according to actual calendar years, chi-square=3.991, df=4, p=0.45. For the 1988 cohort, chi-square=6.783, df=4, p=0.15. For all cohorts grouped according to time since release, chi-square=7.662, df=4, p=0.11. In no instances were inter-year differences in percent annual survival significant. Interestingly, the latter two analyses, which come closest to significance at the p=0.05 level both track survival over the course of time since release, and are therefore more sensitive to differences related to time since release.

The relationship of survival to age, sex, origin (pet or wild), and time in holding pen (0 or 15 days) was analyzed by categorizing survival data in two basic ways, and performing a number of analyses on these data. The first compared numbers of individuals surviving to three years and five years after release, and tested for differences in survival due to the above factors with single factor chi-square analysis and a multi-factor models using stepwise logistic regression.

Based on single factor analyses, there were no significant differences in survival to three or five years past release attributable to sex, origin, or time in holding pen. There were, however, differences due to age: survival of the younger individuals (age class 2) to three years after release was significantly lower, though there was no significant difference in survival to five years after release (Table 27).

Stepwise logistic regression was used to test the relationship of age, sex, origin, and time in holding pen to the number of individuals surviving after three and five years. Only age was found to be significant. For survival to three years, model likelihood ratio chi-square=10.52, df=1, p=0.00, and age chi-square=6.03, p=0.01. For survival to five years, model likelihood ratio chi-square=7.148, df=1, p=0.01, and age chi-square=4.84, p=0.03.

A multi-factor model with all possible two way interactions was tested using stepwise proportional hazards regression. It analyzed survival time distributions and found no significant differences attributable to age, sex, origin, time in holding pen, or any of the possible two way interactions (model likelihood ratio chi-square=2.29, df=1, p=0.13). The only variable entered into the model was age (p=0.11).

Survival time distributions were also analyzed using the parametric PROC LIFEREG (SAS Institute 1990), which tests models of main effects only. A model containing all four main effects (time in holding pen, origin, age, sex) was tested, using the Weibull distribution. None of the four variables were significant (time in holding pen p=0.79, origin p=0.83, age p=0.052, sex p=0.60), though the effects of age approached the p=0.05 significance level.

Differences in survival may be due to differences in known mortality and/or "disappearance" (ie. fate unknown). Percent dead after three years was 47% and 39%, for age class 2 and age class 3+4 respectively. After five years, it was 30% and 45%. These data were analyzed using single factor chi-square tests. Data were the number of individuals known to be dead three and five years after release, and number of individuals disappeared (ie. fate unknown) after three and five years. Differences between age groups in percent dead were not significant. Percent unknown after three years was 47% and 15% for age class 2 and age class 3+4 respectively. After five years it was 70% and 23%. Differences between age groups in disappearance after both three and five years were significant (Table 28), indicating that age-related differences in survival are primarily due to differences in disappearance.

Further analysis of disappearance was carried out using stepwise proportional hazards regression to test for differences in time to disappearance attributable to age, sex, origin, or time in holding pen. A multi-factor model with all possible two-way interactions was tested. Age was the only variable entered into the model and found significant (model likelihood ratio chi-square=7.72, df=1, p=0.01, age chi-square=7.55, p=0.01). A risk ratio of 0.22 indicates that age class 3 individuals had a lower "hazard function" than age class 2, meaning that the older group had a lesser risk of disappearance. This analysis agrees with the above, single factor analysis, in finding a significantly higher rate of disappearance among younger (age class 2) Terrapene.

One additional analysis of time to disappearance was performed, using the parametric PROC LIFETEST. A model containing all four main effects (time in holding pen, origin, age, sex) was tested, using the Weibull distribution. Age was again found to be a significant variable (time in holding pen p=0.76, origin p=0.65, age p=0.01, sex p=0.55) in the distribution of time to disappearance.

Survival of individuals released without radios show a pattern similar to those with radios, with the exception that individuals of unknown fate comprise a larger proportion (Figure 34). Known rate of survival was lowest initially, 44% and 67% in the first two years respectively, increasing to over 90% by the fifth and sixth years respectively (Figure 35). Annual variation in survival rate was significant (chi-square=71.44, df=5, p<0.001).

As with radio-tagged individuals, the relationship of age and sex to survival was analyzed by categorizing survival data in two basic ways. The first compared the number of individuals known to survive to three and five years after release, and tested for differences in survival using both single and multi-factor logistic regression models. Models with the lowest value of the Akaike Information Criterion are considered the best fit (SAS Institute 1990). Based on these analyses, there were no significant differences in survival to three and five years after release due to age or sex (Table 29).

The second method of analyzing the relationship of survival to age and sex utilized survival analysis, ie. proportional hazards regression. In this analysis, survival time (time to death, disappearance, or conclusion of field work) was analyzed relative to the two above potential sources of variation. Because recaptures of animals released without radios were incidental and infrequent, the time scale used for event time is coarser than that used for animals with radios. Years since release, rather than actual number of activity days, is used. For example, if an animal was alive the first spring following release, but dead by the second, the value for event time (time of death) is one.

Stepwise proportional hazards regression analysis was performed on a model containing age, sex, and their interaction. The interaction variable of age and sex was significant (model likelihood ratio chi-square=5.01, df=1, p=0.03, agesex chi-square=4.98, p=0.3), indicating that the higher survival rate seen in young (age class 2) males (Table 29) is significant.

Where possible, causes of mortality were identified as follows;

1. Winter Kill-individuals that entered into but failed to survive hibernation,

2. Pneumonia-animals that exhibited external symptoms of cream colored nasal discharges (Evans 1983),
3. Vehicle related - run over on road by automobiles or by tractors mowing trails and fields, or
4. Unknown.

Causes of mortality in order of importance were winter kill (36%), unknown (32%), pneumonia (20%), and vehicles (12%). The magnitude of winter mortality varied significantly between years, from a high of 38.5% during the winter of 1989-90 to 0% during the winter of 93-94 (Figure 36).

3. B.f. Reproduction

In addition to the observations of courtship and mating noted in the section on Activity, data on various aspects of reproduction were collected during the course of the study. These included palping females for eggs when possible, X-raying of females once in 1992 (30 June 1992) and twice in 1993 (10 June 1993 and 25 June 1993), and recording offspring (ie. young, unmarked Terrapene). These data help define the time period that females are gravid, as well as the nesting season, fecundity rates, clutch size, and annual variation in reproduction of the repatriated Terrapene.

3.B.f.1. Gravid females

There were 19 records of gravid females, based on palping or X-rays. The time period during which gravid females were recorded ranged from June 1st through July 7th, with the majority of records during the last three weeks of June (Figure 37).

3.B.f.2. Nesting season

Only one actual record of nesting was recorded, that of T505 on 22 June 1995. However, for an additional 14 closely monitored individuals, nesting dates can be estimated by bracketing, using the last date they were known to be gravid, and the next subsequent date on which they were not gravid. Estimated nesting dates ranged from 17 June to 10 July, with the majority of nesting occurring during the last half of June and the first week of July (Figure 38).

3.B.f.3. Fecundity rate

Though data are limited, they show that female Terrapene exhibit annual variation in reproductive effort. These data show that some individuals were gravid in all years for which adequate data exist (e.g. T528) whereas others (e.g. T400, T489, T526, T540) were never gravid (Table 30). Several others showed patterns of being gravid in some, but not all, years sometimes on consecutive years (e.g. T351), and sometimes in alternating years (e.g. T210).

Fecundity rates for individuals and by year (Table 30) reflect the variability discussed above plus that due to small sample sizes in most years. However, in 1993, weekly monitoring and X-rays taken on two dates (10 June 1993 and 25 June 1993) provide reasonably comprehensive data on reproductive condition of females. For 1993, 7 of 15 (47%) of females were gravid. This estimate is in close accord with the overall estimate of fecundity of 46%.

3.B.f.4. Clutch size.

Clutch size data were obtained from X-rays of gravid females in 1992 and 1993, and from the nest of T505 in 1995. Clutch size ranged from one to nine eggs, though the one egg recorded for T513 on 30 June 1992 may represent a residual egg rather than the full clutch. The mean clutch size was 5.8 (SD=2.23, n=11). There was no significant relationship between clutch size and carapace length when analyzed by linear regression (r=0.11, p=0.74) or ranked correlation (Spearman correlation coefficient=0.13, p=0.69).

3.B.f.5. Progeny

A total of ten Terrapene offspring were recorded. Their ages (ie. the number of years since hatching year) when first recorded were; one year - one individual, two years - one individual, three years - four individuals, five years - three individuals, and seven years - one individuals. These data indicate that some Terrapene were reproducing successfully by 1988 and that most (8 of 10) records were of individuals HY+3 or older, and occurred in or after 1993 (Table 31).

3.B.g. Home Range

3.B.g.1. Establishment

The traditional definition of home range, "that area traversed by the individual in its normal activities of food gathering, mating, and caring for young" (Burt 1943), does not necessarily fit repatriated animals. Their relocation from a home site to a distant, unfamiliar site is hardly "normal". Their subsequent movements are often highly directional, indicative of homing or dispersal rather than normal movement on a home range. Thus the first aspect of home range is determining the extent to which repatriated animals established home ranges.

For the 53 individuals released with radios, movement and locality data were examined and individuals classified into one of three categories; 1) having left Floyd Bennett Field, 2) established a home range, or 3) died before the occurrence of one of the two above events could be ascertained.

Individuals classified as leaving the site included, 1) those that were tracked off the site, 2) those that were tracked to the perimeter of the site and disappeared subsequently, and 3) individuals that exhibited uni-directional movement prior to disappearing and have been missing for five or more years.

This latter criterion is based on an evaluation of recapture data of Terrapene released without radios. In looking at the time to first "long-term recapture" (recapture alive or dead in a year subsequent to the release year), most first "long-term recaptures" were recorded within a few years of release (Figure 39). These data show that 97% of the first recaptures were within five years of release. After five years, the probability of a first recapture is slight, suggesting that most (though not all) of the unaccounted-for individuals have left the site. Since, for purposes of recapture, missing radio-tagged individuals are the same as turtles without radios, it is reasonable to apply these data to the missing radio-tagged turtles as well. This leads to the conclusion that individuals meeting the conditions number 3 above have most likely left the site.

Individuals classified as having established home ranges are those whose movements show a shift from unidirectional dispersal from the release site to a pattern of relatively short distance, multi-directional movements that remain within a relatively well defined area of the study site. Movements of Turtle 313 illustrate the movements of an individual whose 95% harmonic mean includes the release point (Figure 40, 41), whereas movements of Turtle 389 illustrate an individual whose established home range does not include the release point (Figures 42, 43). Another attribute often useful in identifying this group is the graph of straight-line distance from the release point and activity days since release. For animals that establish home ranges, distance from release point reaches an asymptote and becomes relatively stable for periods of a year or more (Figures 44, 45). Similar graphs for animals that left the study site, or died before outcome could be determined, lack either the asymptote and/or the long-term pattern (Figures 46, 47). Animals classified as establishing home ranges include all individuals remaining alive on the site at the conclusion of the study, as well as individuals that died after establishment of home range.

The third category of outcomes, individuals that died before a determination of dispersal or establishment could be conclusively determined includes individuals that died shortly after release, as well as individuals that died one to two year's post-release.

Of the 53 radio-tagged Terrapene, 13 (24.6%) left Floyd Bennett Field, 25 (47.2%) established home ranges, and 15 (28.3%) died before sufficient data to demonstrate dispersal or establishment were collected. Animals that left the site were radio-tracked for a mean 49.4 days (range 4 - 85, SD=31.7). Animals that died before any outcome could be determined were tracked for an average of 149.7 activity days (range 6 - 322, SD=102.0).

When an individual established a home range is not as easily nor precisely defined as time to disappearance or death. Rather than attempt to precisely estimate this vaguely defined point in time, the year in which an animal's movements met the criteria for home range establishment described above was used to estimate the time to establishment of home range. Of the 25 Terrapene that established home ranges, 17 (68%) did so in the release year, 2 (8%) in the first outyear, 3 (12%) in the second outyear, and 3 (12%) in the third outyear.

3.B.g.2. Home Range Size

Range size for each individual was calculated for two time periods. Total range covers the entire time period for which data are available, and includes all independent, active season points. For each individual, total range begins at the release point, includes all locations recorded while dispersing from the release point, plus all locations recorded after establishment of home range. Total range is thus an estimate of the entire area travelled by each individual following its release, and was calculated for all individuals with a minimum of 10 points.

Home range was estimated for those individuals released with radios that established home ranges, plus 20 additional individuals subsequently fitted with radios in 1992 and 1993. For each, location points from release through the end of the year during which home range was established were not included, since these points represent the animal's post-release dispersal rather than movements on a home range. Thus, home range (*sensu* Burt 1943) was estimated for all individuals having a minimum of ten points recorded subsequent to the year in which it established a home range.

Ranges were calculated using the 95% bivariate normal (95%BVN) method (Jennrich and Turner 1969) and the 95% isopleth of the harmonic mean (Dixon and Chapman 1980). These two methods are not sample size dependent and are often better estimators of the actual utilized area than the minimum convex polygon or range length methods (Ackerman et al. 1990, White and Garrot 1990). The 95% harmonic mean is more sensitive in estimating actual utilized area ("core areas") by excluding outlier points and non-utilized areas. However, since the major works on home range in *T. c. carolina* (Madden 1975, Stickel 1989) use the 95% bivariate normal method, this is the principal method used for comparisons with other populations. HOMERANGE (Ackerman et al. 1990) was used to calculate 95%BVN, and 95%HM were calculated using RANGES IV (Kenward 1990). Due to heterogeneity of variance in the data on home range size, all statistical analyses of variation in home range size is based on log transformed (base 10) data.

The mean 95% bivariate normal total range was 22.58 ha (SD=24.90, n=65). Individuals ranged from 0.17 to 107.43 ha (Table 32). Total range of females (mean=23.41 ha, n=35) was not significantly different from that of males (mean=21.61 ha, n=30) (t=1.20, df=63, p=0.23). Total range of young adults (age class 2) (mean 19.33 ha, n=21) was not significantly different from that of middle-age and older adults (age class 3+4) (mean 24.13 ha, n=44), (t=-0.70, df=63, p=0.49).

The mean 95% harmonic mean total range was 8.50 ha (SD=10.79, n=65). Individuals ranged from 0.04 to 48.03 ha (Table 32). Total range of females (mean=9.15 ha, n=35) was not significantly different from that of males (mean=7.71 ha, n=30) (t=0.97, df=63, p=0.33). Total range for young adults (age class 2) (mean=4.64 ha, n=21) was not significantly less than that of middle-age and older adults (age class 3+4) (mean=10.34, n=44) (t=-1.72, df=63, p=0.09).

The mean 95% bivariate normal home range was 9.77 ha (SD=9.0833, n=40). Individuals ranged from 0.57 to 39.82 ha (Table 33). Home range of females (mean =11.43 ha, n=25) was not significantly different from that of males (mean=7.00 ha, n=15) (t=1.45, df=38, p=0.16). Home range for young adults (age class 2) (mean 11.81 ha, n=12) was not significantly different from that of middle-age and older adults (age class 3+4) (mean 8.90 ha, n=28), (t=0.12, df=38, p=0.90).

The mean 95% harmonic mean home range was 4.82 ha (SD=6.97, n=40). Individuals ranged from 0.24 to 42.57 ha (Table 33). Home range of females (mean=5.51 ha, n=25) was not significantly different from that of males (mean=3.67 ha, n=15) (t=0.65, df=38, p=0.52). Home range for young adults (age class 2) (mean=2.67, n=12) was not significantly different from that of middle-age and older adults (age class 3+4) (mean=5.74, n=28) (t=-1.16, df=38, p=0.25).

Possible variation in home range size due to the two factors, age and sex, and their interactions were analyzed using the SAS General Linear Model. For 95% harmonic mean estimates of home range, neither the two factor with interactions model, nor the two factor without interactions were significant (p=0.51 and p=0.31 respectively). For 95% bivariate normal estimates of home range size, neither the two factor with interactions model, nor the two factor without interactions were significant (p=0.55 and p=0.36 respectively).

The influence of nesting movements on the home range size of females was analyzed by comparison between females known to have been gravid at least once during the time period of the home range estimate and those not known to be gravid. For 95% harmonic mean estimates, home range of gravid females (mean=8.91 ha, n=11) was significantly larger than non-gravid females (mean=2.83 ha, n=14) (t=-2.52, df=23, p=0.02). For 95% bivariate normal estimates, home range size of gravid females (mean=17.16 ha, n=11) was also significantly larger than that of non-gravid females (mean=6.93, n=14) (t=-2.70, df=23, p=0.01).

Home range size of non-gravid females were also compared with those of males. The 95% harmonic mean home range of males (mean=3.67 ha, n=15) was not significantly different from that of non-gravid females (mean=2.83 ha, n=14) (t=0.52, df=27, p=0.61). Similarly, the 95% bivariate normal home range of males (mean=6.99 ha, n=15) was not significantly different from that of non-gravid females (mean=6.93 ha, n=14) (t=-0.15 df=27, p=0.88).

3.B.g.3. Home Range Stability

Inter-year stability of home ranges was evaluated by multivariate methods (White and Garrot 1990). For each individual that had established a home range, multi-variate analysis of variance (MANOVA) was performed to test for changes in home range geographic centers (mean X and Y coordinates). Tests were performed between years for which a minimum of 10 data points existed and there was a minimum of two months overlap in coverage between years (Madden 1975). MANOVA tested the model that variation in the X and Y coordinates was dependent on the independent variable YEAR. It provided a test of each dependent variable, as well as a test of the hypothesis of no overall year effect.

Seventeen different individuals (eight female, nine male) provided 25 inter-year comparisons. Of these 17 individuals, 13 provided one inter-year comparison, one provided two, two provide three, and one individual provided four inter-year comparisons. Of the 25 comparisons, 15 demonstrated significant ($p<0.05$) inter-year differences in geographic centers of home range and the remaining 10 did not (Table 34).

Of the 15 instances of significant change, males accounted for eight and females for 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 these results suggest that males tended towards stabler home ranges than females, these differences were not significant (chi-square=0.87, df=1, p=0.40).

Distance between geographic centers of home ranges ranged from 7.1 to 46.0 m (mean=23.0, SD=12.69) in instances where there was no significant inter-year shift. In instances where there was significant inter-year shift, distances between geographic centers ranged from 16.5 to 202.9 m (mean 99.7, SD=60.35). Differences between instances of home range shift versus home range stability in this parameter (inter-year distance between geographic centers of annual home range) were significant (p=0.001). Among the 15 instances of home range shift, there were no differences in the magnitude of shift due to sex (t=1.04, p=0.32).

3.B.g.4. Stability of Hibernacula

Distance between hibernacula used in consecutive years by individuals that had established home ranges was calculated. Only hibernacula used after home range establishment were used. Distance between consecutive year's hibernacula varied between and within individuals (Table 35). Distance ranged from 0.3 to 332.1 m, with an overall mean distance of 97.6 m (SD=89.91, n=44). A number of individuals with relatively small inter-hibernacula distances (eg. T210, T310, T323, T389, T400, T489, T584) provide examples of hibernation site fidelity, essentially hibernating in the same habitat patch in two or more consecutive years. Though variable, most inter-hibernacula distances were less than 100 m (Figure 48).

Turtle T389, which hibernated in the same basic spot for five consecutive years, provides the best example of hibernation site fidelity. Yet, in the winter of 1993-94, it hibernated at a site over 200 m from the previous five winter's, demonstrating the highly variable nature of this phenomenon.

Variability of inter-hibernacula distances was analyzed using SAS General Linear Model (Proc GLM). A two way model incorporating Individual Turtles and Time Periods as sources of variation was tested. Neither the model, individuals, nor time periods were found to be significant (p=0.68, p=0.64, and p=0.91, respectively)

3.B.h. Habitat Relationships

Habitat use was analyzed using a habitat map prepared from a 1992 aerial photograph of Floyd Bennett Field. Based on the photograph (scale 1:2400) and extensive ground truthing, Floyd Bennett Field's vegetation was mapped in accordance to procedures outlined in Lent and Litwin (1989) and digitized (Lent and Cook, unpublished). The vegetation map was then converted, using IDRISI software (Eastman 1993) into a simpler habitat map that reflected major structural elements (Figure 3).

Since repatriated animals dispersing from a release point have not necessarily selected the habitat they were recorded in, only animals that had established home ranges were used for habitat analysis, and only those points recorded subsequent to home range establishment were used. These points represent the habitats used by the repatriated Terrapene after they have had an opportunity to establish themselves at the release site. Habitat use was determined by overlaying locality coordinates for individual animals onto the habitat map and extracting habitat values for each point (Table 36).

Determination of available habitat was based on habitat types within an area used by all turtles (Doroff and Kieth 1990), rather than Floyd Bennett Field in its entirety. Since much of Floyd Bennett Field was not reached by radio-tagged turtles, the validity of considering the entire site as available habitat was questionable. For all radio-tagged Terrapene, all points on Floyd Bennett Field were combined and the minimum convex polygon (Mohr 1947) enclosing them calculated. IDRISI was then used to calculate the area of each habitat type within the polygon, thereby providing the available habitat (Table 37).

Chi-square analysis of habitat preference was carried out for each individual, and to test for differences between individuals. For those individuals deviating from random use, specific habitats preferred or avoided were determined by calculating the 95% confidence interval for the proportion of time each individual used each habitat type. If the available proportion of a given habitat fell within the 95% confidence interval of proportionate use, there was neither preference nor avoidance. If the lower limit of the interval exceeded availability, there was preference and conversely, if the upper limit was below the available proportion, there was avoidance (White and Garrot 1990).

For all analyses, runway was dropped as a habitat type. It's use was never recorded in the course of radio-tracking and it is too artificial to be reasonably considered a habitat type. In case of the lawn, shore, and wetland habitats, the relatively small amounts of these habitats would lead to low values of expected cell frequencies during chi-square analysis. However, since nearly all of these cells had observed values of zero, the contribution to an individual's total chi-square resulting from this situation was small. Analyses originally conducted with these habitat types would not be altered by deleting these habitats.

In the initial analysis, based on seven habitat types, there were significant differences between individuals (chi-square=1231.3, df=195, p<0.001). Eleven individuals used habitat randomly, and 29 showed significant departure from random (Table 38). Among these 29, there was considerable variation in preference and avoidance, though lawn, shoreline, and wetland habitats were highly avoided. Grass-herb dominated habitats were also avoided. Phragmites-dominated habitats were avoided by most individuals, but seven individuals showed a significant preference. The two woody plant dominated habitats, deciduous forest and shrub were the most frequently preferred and least avoided.

Summary statistics for the entire sample of individuals were calculated in a number of ways. Summation of individual chi-squares and their degrees of freedom provides an overall test of habitat selection (White and Garrot 1990). As a group, habitat use differed significantly from random (chi-square=1578.4, df=240, p<0.0001).

For the 29 individuals that did not use habitat randomly, I developed an index of preference or avoidance. Preference was scored "+1", avoidance "-1", and neutral "0". For each habitat, scores were summed and divided by the total number of scores, producing an index that potentially ranged from -1 (total avoidance) to +1 (total preference). Results of this index are similar to those described above. Open habitats were highly avoided, <u>Phragmites</u>-dominated habitats avoided, deciduous forest barely avoided and shrub habitat barely preferred (Table 38).

Pooling of data over animals was also performed, though this method has the potential problem of masking significant deviations from random by combining data from individuals with opposing preferences (White and Garrot 1990). However, heterogeneity chi-square was calculated and where non-significant, analysis of pooled data is justifiable (Zar 1984). Since each individual was represented by different numbers of points, data were standardized to provide each individual equal weight. In this case, results of pooling indicate that habitat use was not random, and that deciduous forest and shrub habitat was preferred, and all others avoided (Table 38).

There were 21 instances where one of the two woody-dominated habitats was avoided. In 15 of them, avoidance of one woody habitat was coupled with preference for the other. Nine individuals avoided forest while preferring shrub, and six avoided shrub while preferring forest. On Floyd Bennett Field, due to the relative youth of the landscape, the forested habitats are still in the early stages of succession. Shrub and forested habitats overlap in species composition and differ principally in height. This consideration, in conjunction with the above results suggested that Terrapene were not differentiating between these two habitats. Accordingly, shrub and forest were combined into a single habitat, woody-dominated, and a second analysis performed.

Analysis of habitat based on six habitat types indicated that there were significant differences between individuals (chi-square= 677.0, df=156, p=0.000). Nineteen individuals did not deviate significantly from random habitat use (Table 39). For the remaining 21, patterns of preference and avoidance were similar to the initial analysis. Lawn, shoreline, and wetland habitats were universally avoided, and grasslands were also highly avoided. Phragmites-dominated habitats were avoided by 12 individuals, but preferred by seven. Woody-dominated habitats were preferred by 13 of the 21 individuals. Of the eight individuals that did not prefer woody habitat, seven showed a preference for phragmites.

As a group, habitat use differed significantly from random (summed chi-squares=705.7, df=200, p<0.0001). Analysis based on pooled data (heterogeneity chi-square was non-significant) also showed that habitat use was not random. Both this analysis and indices of preference show that woody-dominated habitat was preferred, and all others avoided (Table 39).

There were significant differences between the sexes (chi-square=45.782, df=4, p<0.001) as well as among females and among males (Table 40). Thirteen of 25 females and six of 15 males used habitat randomly. Collectively, females highly avoided lawn, shoreline, and wetlands, avoided grassland-herbaceous habitats, were neutral to slightly avoided Phragmites, and showed a moderate preference for woody habitats. Though males and females had qualitatively identical patterns of preference and avoidance, the significant differences between the two sexes are in the magnitude of their preferences and avoidances. Males showed a stronger preference for woody habitat, and a stronger avoidance of grassland-herbaceous and Phragmites-dominated habitats (Table 40).

Habitat use by females that nested was analyzed by dividing females into those known to have been gravid and those not gravid. For each of these two groups habitat use was non-random, and differences between these two groups were significant (chi-square=206.63, df=4, $p<0.001$). The principal difference in habitat use was that gravid females avoided Phragmites-dominated habitat whereas non-gravid females showed a preference for this habitat (Table 40).

Seasonal use of habitat was looked at in two ways. The first uses the approach of Doroff and Kieth (1990) and divides the activity year into four time periods that reflect both calendar and functional seasonality. The four "seasons" were Early Spring (initiation of activity to 21 April), Late Spring/Early Summer or Nesting (22 May to 15 July), Summer (16 July to 21 September) and Autumn (22 September to hibernation). The second approach follows that of Madden (1975) in which the activity year is divided into calendar months. Since activity periods differed between individuals, there were small numbers of observations made in the first and last months for which there are data, April and November. Data from these months were grouped with the data for May and October, respectively.

There were no significant differences in between-season or between-month use of habitat when tested for all individuals, by sex, or for gravid v.. non-gravid females (Table 41, 42). Seasonal use of habitat largely reflected the same patterns seen in the overall analysis. However, females tended towards greater variability in habitat use over the course of the activity year than males, with gravid females coming the closest to the critical values for p=0.05.

Winter or hibernation habitat use was analyzed, using data from radio-tagged animals tracked to hibernacula. Based on all available data, woody habitats and Phragmites-dominated habitats accounted for nearly all hibernacula (Table 43). Choice of hibernation habitat was not random (chi-square=42.17, df=6, p<0.001). Woody habitats were significantly preferred, Phragmites-dominated habitats were neutral, and all others were avoided. Though as a whole, the population was neutral towards Phragmites-dominated habitats, a number of individuals (eg. T271, T313, T513, T540) consistently hibernated in Phragmites.

A similar analysis was performed using only individuals that had established home ranges and only hibernacula used after home range establishment. Results were essentially identical (chi-square=37.47, df=6, $p<0.001$).

In the ten cases of winter kill recorded, six occurred in woody habitat, three in Phragmites, and one in grass/herbaceous. There was no significant relationship between winter kill and hibernation habitat (Fisher's exact test, $p=0.18$).

Chapter 4. DISCUSSION

4.A. Painted Turtle

4.A.a. Survival

Using averages derived from 16 studies of freshwater turtles (representing 9 species and 3 families) Iverson (1990) described patterns of annual survival in freshwater turtles. In general, annual survival in freshwater turtles can be characterized as relatively low (ca. 20%) during the egg and hatchling stage, moderately high (ca. 67%) in juveniles, and high in subadults (ca. 84%) and adults (ca. 88%).

In *C. picta*, annual survival has been estimated for a number of populations. These studies, taken as a whole demonstrate the age-related differences in survival noted above, as well as geographic and temporal variation. In Nebraska, annual survival of adult females averaged 81.5% (Iverson and Smith 1993). In a Virginia population studied over three seasons, annual survival was estimated at 45.7% for juveniles, 94.4% for immature females, 95.6% for adult males, and 96.3% for adult females (Mitchell 1988). In a southeast Michigan population, annual survival of hatchlings to age one increased from 8% during the period 1953-1957 to 18% during the period 1968-1972. For these same two time periods, annual survival rates of adults decreased from 83% to 76% (Wilbur 1975). In a southwest Michigan population studied in 1964 to 1966 and again from 1980 through 1989, annual survival rates of juveniles increased steadily with age, from 21% at age one to 51% at age five. Adult females ranged from 29% to 50% whereas estimated annual male survivorship ranged from 65% to 83% (Frazer et al. 1991). In a Dix Hills, Long Island, N.Y. population, studied over an 18 year period, annual female survivorship ranged from 85.7% to 100%, whereas male survivorship ranged from 54.2% to 97.5%. In this population, low male survival coincided with attainment of sexual maturity and increased overland movements, then fluctuated thereafter (Zweifel 1989).

Annual survival of C. picta repatriated to Return-A-Gift Pond (RAG) exhibited annual survival rates well within this range of reported values. Generally ranging from 85% to 100% for adults, with female survival slightly higher than male, the C. picta in this study more closely resembled the populations from Nebraska, Virginia and Long Island than those of Michigan. However, Frazer et al. (1991) suggest that their methodology may have underestimated actual survival. The other Michigan population appears somewhat unique in that predation by raccoons (Procyon lotor) is an important adult mortality factor (Wilbur 1975) though Seigel (1980) also noted high predation by raccoons on female diamondback terrapins (Malaclemmys terrapin) in Florida.

Thus, comparisons of survival between these populations suggest that adult survival rates are fairly comparable, except in populations with high predator pressures. For those individuals repatriated to RAG pond, the data indicate that repatriation did not adversely affect survival.

In comparing release treatments, turtles held for 10 days in a pen had lower survival, through not significantly so, than individuals released immediately into the pond, or escaped from the pen (Table 3). For the first inter-year period (1990-1991) survival of animals released immediately was 95.5% whereas that of animals held in the pen for 10 days was 76.2%. This suggests that an in situ holding pen may contribute to reduced survival. While a redesign of the holding pen could conceivably reduce its negative impact, the high survival of animals released directly into the pond obviates the need for one.

4.A.b. Homing and Dispersal

Homing in *C. picta*, as well as many other species of turtles, has been well documented (eg. Cagle 1944, Williams 1952, Gould 1959, Ernst 1968, 1970, Carroll and Ehrenfeld 1978, Madden 1975). While homing was not directly investigated, since the extent to which repatriated animals home can affect the success of repatriation efforts (Berry 1986), it has direct bearing here.

Following repatriation (or any relocation) animals may remain at the release site or disperse from it. Dispersal from the site may involve random movements, homing, or movements oriented in a direction other than home. Thus, losses to the population of repatriated individuals may be either due to mortality or some form of dispersal.

Cagle (1944) relocated 89 _Pseudymys_ _scripta_ to a pond "many miles distant" from their home site. Thirty were still present the following year, but after two years all but "very few" could be accounted for at the release pond. Similar results were obtained with 164 _C_. _picta_, leading Cagle (1944) to conclude that "Turtles transferred to a strange water body appear to wander at random". However, Cagle also documented successful return of relocated animals, and concluded that turtles display some homing behavior. Moreover, others were recaptured in a third pond, which was neither the home nor the release site. Regardless of whether their movements were homeward directed or random, Cagle's data suggest that most relocated _Pseudymys_ or _Chrysemys_ will not remain at the release site.

Williams (1952) showed that _C_. _picta_ successfully homed up to 620 m when relocated within a large lake. Effects of distance relocated on homing was shown by Emlen (1969). In tests of dispersal direction, individuals displaced 100 m from their pond dispersed pondward, whereas when displaced 1.6 km from the pond they dispersed at random. From these and related tests, conducted on sunny and cloudy days, Emlen (1969) concluded that homing was based on use of local landmarks rather than sun-compass orientation. If true, this would suggest that animals repatriated relatively long distances would not be expected to home. However, several other studies have shown that C. picta are able to employ sun-compass orientation (Gould 1959, DeRosa and Taylor 1978), and should be able to home from greater distances than suggested by the findings of Emlen (1969).

These studies provide contradictory results with respect to the mechanisms of homing and the ability of Chrysemys to home from distances of 1.6 km or more. Yet whether one accepts sun-compass orientation, with the implication that this mechanism would be employed by repatriated turtles to home (or at least attempt to do so) or the random dispersal mechanism suggested by the experiments of Emlen (1969) and seemingly demonstrated by Cagle (1944), the predicted outcome would be the same; the overwhelming majority of repatriated turtles would be expected to leave the release site.

Results obtained at RAG pond are not consistent with the above prediction. Over the course of the study, no dead Chrysemys were recorded, suggesting that most (but not necessarily all) animals left the pond/population via emigration rather than actual mortality. However, the rate at which they left the population (10.9%, 12.2%, and 2.3% annual rates for 1990-1991, 1991-1992, and 1992-1993 respectively), is much less than would be expected.

The high percentage of individuals that remained at RAG may be a result of the large distance they were repatriated and its impact on their homing ability (see Emlen 1969). However, most studies demonstrate support for sun-compass orientation in C. picta (DeRosa and Taylor 1978), suggesting that the repatriated Chrysemys should have been able to attempt homing.The results obtained indicate that for most of the Chrysemys repatriated to RAG, either they remained in the pond or dispersed (randomly or homeward directed) and then returned. Data are not available to determine the frequency of each of these three possibilities.

Most of the major studies of C. picta (Cagle 1944, Wilbur 1975, Tinkle et al. 1981, Gibbons, 1968. Frazer et al. 1991, Zweifel 1989) took place at sites containing a complex of several adjoining ponds and wetlands, connected at least part of the time. These studies demonstrated varying degrees of movement between water bodies, generally on a seasonal basis or in response to pond drying. Animals leaving their primary pond in response to drying generally returned when conditions were favorable once again (Cagle 1944, Zweifel 1989).

At Floyd Bennett Field, RAG pond is the only permanent freshwater body present. Even though it fluctuates by ca. 2 m in water depth and decreases in late summer to ca. 10% of its springtime area, it retains water even in dry years. Other wetlands on Floyd Bennett Field consist of sheetwater marshes that dry out annually, even in wet years. Thus, since RAG pond is the only suitable habitat on Floyd Bennett Field for Chrysemys, the possibility exists that repatriated individuals left the pond initially and subsequently returned. Since their movements were not monitored with radio-telemetry, there is no way of evaluating this possibility. However, observations at nearby Jamaica Bay Wildlife Refuge, also involving repatriated Long Island, NY Chrysemys provide some support for this. At Jamaica Bay Wildlife Refuge, some repatriated individuals released in one pond were observed in another pond, ca. 150 m away. Thus repatriated Chrysemys appear to distribute themselves among the available habitats and at Floyd Bennett Field available habitat is limited to RAG pond.

In another successful repatriation of Long Island Chrysemys, nine individuals were repatriated an average of 50.4 km (range 25.3 to 57.4). By the year following repatriation, one had been lost track or, one was D.O.R. and a third was captured in another pond, a minimum of 600 m away (Zweifel 1989, Zweifel pers. comm.). Another individual also moved to this same pond by the second year following repatriation. The balance of individuals remained in the release pond.

Thus the results at Floyd Bennett Field, as well as those of Zweifel (1989 and pers. comm) and Cagle (1944) suggest that when Chrysemys are repatriated distances from which returning home would be unfeasible, most simply disperse into available local habitats.

4.A.c. Growth

The general pattern of growth in chelonians is one of rapid growth among the youngest age classes, with declining rates and increments of growth after the onset of sexual maturity (Auffenberg and Iverson 1979, Bury 1979). Superimposed upon this generalized pattern of age-related variation in growth is variation due to a number of other factors that broadly reflect evolutionary and ecological differences between species, sub-species, populations, and individuals.

In reviewing the extensive literature on growth in C. picta, Zweifel (1989) noted that variation in growth rates (and maximum sizes attained) has been attributed to geographic variation, sub-specific variation, diet, habitat, substrate, and their interactions. Essentially, members of the northerly distributed sub-species, particularly C. p. belli, are largest and exhibit the greatest rates of growth. Within subspecies, larger size and more rapid growth was found in populations in habitats with muddy substrate, as opposed to sandy, and in populations characterized by a carnivorous as opposed to an herbivorous diet. Thus, comparisons between populations must take these variables into account. Also complicating comparisons is the fact that the individuals repatriated to RAG were too old to be aged by annuli. They were primarily adults that could only be grouped into size categories.

Patterns of growth in C. picta at RAG were comparable to those reported in the literature. Growth was greatest among the smaller size categories, with little measurable growth in large adults of either sex (Figures 4, 5, 6). Greater growth in smaller females (eg. the 80-89, or 90-99 mm size categories) as opposed to males, reflects reduced growth in males after sexual maturity. Zweifel (1989) estimated size at sexual maturity in his population of Dix Hills. Long Island C. picta to be 80 mm for males and 110 mm for females. Annual variation in growth appears to be correlated to May-August rainfall amounts, which Zweifel (1989) reported to be an important environmental correlate of growth.

Among the many studies of growth in C. picta, those most comparable to this study population are pond and marsh dwelling C. p. picta X C. p. marginata intergrades in southeastern Pennsylvania (Ernst 1971a), and pond dwelling, predominantly C. p. picta on Long Island, NY (Zweifel 1989). Compared to those in southeastern Pennsylvania, C. picta at RAG experienced a higher rate of growth. Differences were greatest between the smaller size categories, particularly between females (Table 44).

To facilitate comparison with the Long Island population studied by Zweifel (1989), data on the mean plastron length at the end of growth years (Table 1 of Zweifel 1989) were used to estimate the annual rates of growth by size category and sex. This comparison indicates that growth rates were, in general, roughly comparable between RAG and Zweifel's population, though males between 100-109 and 110-119 mm grew at about half the rate at RAG (Table 44).

During the five year period covered by his study, Ernst (1971a) reported that growth season rainfall was below average, though he provides no data on the extent of the deficit. At RAG, growth season (May-August) rainfall was slightly above average in 1991 and 1992, and dramatically below average in 1993 (Table 7). For the three season period it averaged 34.6 cm, which is slightly (1.1 cm) below the long term mean of 35.7 cm. Differences between the Pennsylvania population, and RAG may be the result of the below average rainfall reported by Ernst (1971a). Over the course of the 18 seasons which Zweifel's study covered, there was a three year drought. For the entire period, growth season rainfall averaged 33.6 cm, which is also slightly (2.1 cm) below the long term mean.

For all practical purposes, the RAG and Dix Hills, L.I. populations of C. picta experienced similar growth season rainfall. The general comparability in growth rates between the two populations indicates that the individuals repatriated to RAG were able to establish themselves at this site and forage at rates comparable to individuals not subject to repatriation.

4.A.d. Reproductive Output

Reproductive ecology has been extensively studied in fresh water turtles in general and C. picta in particular. These studies detail variation in such parameters of reproduction as absolute and relative (body size adjusted) egg size and mass, clutch size and mass, clutch frequency, and annual reproductive output. Factors correlated with variation in these parameters include size, sub-species, latitude, elevation, climate, and food quantity and quality. From these studies, the following generalizations regarding intra-specific patters of variation in reproduction have been drawn.

1. Clutch size is positively correlated with body size. This relationship exists within populations (Gibbons 1982, Gibbons et al. 1982, Mitchell 1985, Iverson 1992, Iverson and Smith 1993), as well as between populations (Gibbons and Tinkle 1969).

2. The above relationship notwithstanding, clutch size is highly variable, with variation within individuals equal to that between individuals of a population (Gibbons 1982). The extent to which variation in clutch size is due to body size also varies. In a Virginia population of _C. p. picta_, body size accounted for 62.1% of the variation in clutch size (Mitchell 1985), whereas it accounted for only 6.25% in a Nebraska population of _C_. _p_. _belli_ (Iverson and Smith 1993). This variation may be attributed to variation in resource availabilities (Gibbons et al. 1982, Mitchell 1985, Iverson and Smith 1993).

3. Variation in clutch size between nearby populations may be the result of dietary differences. Populations with highly carnivorous diets have larger clutch sizes than herbivorous ones (Gibbons and Tinkle 1969).

4. In a population, there is no significant annual variation in mean clutch size (Gibbons 1982, Schwarzkopf and Brooks 1986).

5. Within a population, females may lay more than one clutch of eggs per year. In C. picta there is direct evidence of individuals laying two and three clutches, and possibly four (Snow 1980, Iverson and Smith 1993). Clutch frequency varies annually within a population, as well as between populations. Since annual reproductive output equals mean clutch size multiplied by clutch frequency, and mean clutch size is less variable, variation in clutch frequency is the dominant influence in variation in annual reproductive output (Gibbons 1982, Iverson and Smith 1993).

6. Between populations of C. picta, clutch frequency is inversely correlated with latitude. Turtles at high latitudes have shorter nesting and growing seasons, which limits the number of clutches that can be produced and incubated. This favors the production of fewer, relatively heavier clutches, and may produce selective pressures for larger body size (Iverson and Smith 1993).

7. Within a population, annual reproductive output, or total fecundity, is positively correlated with measures of body size and mass. However, after adjusting for size, the relative annual reproductive output, was not correlated with size (Iverson and Smith 1993).

8. Across populations of C. picta, size-adjusted annual reproductive output is positively correlated with clutch frequency, and inversely correlated with age at maturity (Iverson and Smith 1993).

9. Among individuals producing more than one clutch in a season, the later clutches tend to be smaller than the earlier (Gibbons et al. 1982, Iverson and Smith 1993).

In summary, these patterns produce a model of variation in life history parameters in which painted turtles in lower latitudes (southern populations) mature at earlier ages and smaller sizes, producing relatively larger but fewer eggs in a clutch, but more clutches annually, than do turtles in high latitude (northern populations) (Iverson and Smith 1993). Since relative annual reproductive output is greatest in populations with high clutch frequency and early maturity, typical of low latitude and early maturing is correlated with shorter longevity (Iverson 1992), it would appear that the shorter-lived southern individuals compensate for reduced longevity by increasing their relative annual reproductive effort.

Considering the above discussion, comparison of reproductive parameters of the RAG C. picta to other populations must be made carefully, using only those populations most similar geographically and ecologically. Also, data from RAG represent only 1993, and provide no measure of annual variation.

Further complicating interpretation of reproductive data in RAG C. picta are uncertainties regarding state of sexual maturity in some females, and differences in methodology among studies. Zweifel (1989) considered all females with plastron lengths greater than 110 mm to be adults. On this basis 20 RAG females X-rayed in 1993 were considered to adults, and only 15 of them were shown to produce eggs. However, four of the five females that did not produce eggs in 1993 are the four smallest individuals, ranging in plastron length from 112 to 121 mm. The smallest individual confirmed gravid was 125 mm (Table 8).

Considering that local inter-population differences in size can be significant (Gibbons and Tinkle 1969), that maximum size and size at maturity are positively correlated (Hart 1982, MacCulloch and Secoy 1983), and the maximum size of the turtles collected from three separate Long Island populations and repatriated to RAG (Table 44) exceeded those reported by Zweifel (1989), it suggests that the size at sexual maturity for these Long Island individuals would be larger than in the Dix Hills, Long Island population studied by Zweifel.

However, evidence also exists that not all adult females nest every year (Tinkle et al. 1981), and in particular young adults may skip a year (Christens and Bider 1986). The fifth "adult" not gravid in 1993, female number 210, had a plastron length of 142 mm and was gravid in 1992, thereby confirming the findings of Tinkle et al. (1981) (Table 8). While impossible to be positive, the relationship between maximum size and size at maturity, plus the fact that all four questionable individuals were below the smallest size shown by X-rays to be mature, and they were never found to contain eggs, leads me to conclude that these four smaller females were probably not sexually mature.

For purposes of estimating fecundity rates and clutch frequency, only females known to be sexually mature will be considered. Thus, a more reliable estimate of fecundity rate is that 94% (15/16) of adult females nested in 1993. Based only on known adults, this provides a minimum known clutch frequency of 1.44 clutches/year which, when multiplied by a mean clutch size of 7.52, provides a minimum known total fecundity of 10.83 eggs/year/adult female. For two reasons, even this is likely an underestimate. First, data provided by and cited in Iverson and Smith (1993) indicate that egg production in C. picta extends into mid-July. An additional round of X-rays in mid-July 1993 might well have provided evidence of additional second clutches. Secondly, three females that were gravid on 28 May 1993 were not recaptured for X-rays on 26 June 1993. Of those individuals that were available on both those dates and gravid on the first, 70% of them were also gravid on the second. Thus, two of these three females (not X-rayed on 25 June 1993) probably produced a second clutch, making the estimated clutch frequency 1.56 clutches/year, and estimated total fecundity 11.73 eggs/year/adult female.

Fecundity data for RAG C. picta (latitude 40.5° North, elevation 5 m) are generally comparable with those populations most similar taxonomically, geographically, and ecologically. The best estimates of mean clutch size among nearby populations of C. picta are 6.8 (Zweifel 1989, using a composite sample from published records from Connecticut and Long Island), and 7.0 for a sample collected throughout Connecticut (Klemens 1993). For a Virginia population of C. p. picta (latitude 38° North, elevation 70 m), mean clutch size was 4.2 and "at least some females lay two clutches in a single season" (Mitchell 1985). Using Mitchell's data, Iverson and Smith (1993) estimated total annual fecundity of this population at 8.2 eggs/adult female. This may be an overestimate, since it is based on all females double clutching.

In a Pennsylvania population of C. p. picta x C. p. marginata (latitude 40° North, elevation 140 m) mean clutch size was 5.1 (Ernst 1971b). Clutch frequency was originally reported as one, but it has been subsequently suggested that this is an underestimate (Iverson and Smith 1993). If clutch frequency of one is an underestimate, a frequency of two may be an overestimate, meaning that total annual fecundity probably lies somewhere between 5.1 and 10.2 eggs/adult female.

In a Michigan population of C. p. marginata (latitude 43° North, elevation 280 m), mean clutch size was 7.6, with only 50-70% of adult females nesting, and 6% (of the total) double clutching (Tinkle et al. 1981). Clutch frequency and total fecundity of this population was estimated at 0.8 and 6.1 respectively (Iverson and Smith 1993). This is likely an underestimate since Tinkle et al. (1981) suggest that they overestimated the number of adult females present, which would underestimate clutch frequency.

More distant geographically and taxonomically, though not latitudinally, are populations in Illinois and Nebraska. In a C. p. belli x C. p. marginata population in Illinois (latitude 39.5° North, elevation 210 m), mean clutch size was 8.7, clutch frequency was 2.34, and total fecundity 20.4 (Moll 1973). In a southwest Nebraska population of C. p. belli (latitude 40° North, elevation 950 m), mean clutch was 7.6, clutch frequency 1.8, and total fecundity 14 (Iverson and Smith 1993). In another Nebraska population of C. p. belli (latitude 42° North, elevation 1165 m), mean clutch size was 13.9, clutch frequency was 2.8 and total fecundity 38.9 (Iverson and Smith 1993).

These comparisons, once geography and taxonomy are accounted for, indicate that the reproductive output of the C. picta repatriated to RAG compares favorably with populations not subject to repatriation. Patterns of variation within the RAG population, such as the significant positive relationship between size and total fecundity and larger first clutches, are consistent with those reported for naturally-occurring populations. Moreover, since data were collected in 1993, and repatriation occurred in 1990, it is not likely that the energy required to reproduce in 1993 represents residual energy from natal ponds. By the end of a growing season, female C. picta contain a set of large and small ovarian follicles. The large set (representing the first clutch of the next year) contain 50% of their final energy content, whereas the small set (representing either the next year's second clutch or a clutch to be deposited in the year after next) contain 11% of their final energy content (Congdon and Tinkle 1982). Based on these estimates, 50% of the energy of the first clutch, and 89% of the energy of the second clutch was acquired in the same year as oviposition. While energy acquired and stored in the year prior to oviposition is significant, energy acquired and allocated to reproductive effort beyond the next year is minor. Thus the energy invested into reproduction in 1993 had to have been acquired following repatriation to RAG.

4.A.e. Habitat Suitability

While no direct measurements of the habitat were taken, inferences regarding its suitability for C. picta, and thus the feasibility of creating habitat, may be drawn from the conclusions regarding growth and reproductive output. From the perspective of the habitat, the fact that the C. picta inhabiting RAG pond acquired energy at rates comparable with naturally-occurring sites, as evidenced by growth rates and reproductive output, indicates that it provided suitable habitat. Records of hatchlings, beginning in 1993, indicate that successful nesting was occurring.

Many instances of C. picta and other aquatic turtles successfully utilizing human-created ponds and marshes have been noted in the literature (eg. Cagle 1994, Kofron and Schreiber 1987, Mitchell 1985, Ernst and McDonald 1989, Christy et al. 1974, Klemens et al. 1992). The commonest mechanisms of creation are damming of streams and creation of farm ponds and other impoundments, such as cooling ponds and sewage lagoons. These instances attest to the adaptability of

C. picta to a wide range of different habitats, provided that their fundamental requirements of slow moving, shallow water, with soft bottom, aquatic vegetation, and basking sites (Ernst and Barbour 1971) are met.

In all these instances, the populations present in these human-created habitats appear to be the result of natural colonization or expansion of an existing population, both spatially and numerically, into the created habitat. In one account, C. picta colonized a small pond within three years of its creation (Zweifel 1989). What distinguishes the present study from these examples is the fact that the turtles in RAG did not colonize the site naturally. While there are some accounts of successful repatriation in C. picta (Zweifel 1989), and probably many more undocumented instances, the work done at RAG is unique in that it involves both repatriated turtles and a human-created pond.

4.A.f. Conclusions Regarding C. picta at RAG

Data collected during a three year period show that repatriated C. picta remained at the release site, and experienced rates of survival, growth, and reproduction comparable to populations not subject to repatriation. Such short-term success, though not proof of long-term success, is encouraging, and suggests that long-term success will occur.

Certainly, there is little evidence to suggest that the opposite of success, failure, has occurred.

4.B. Box Turtle

4.B.a. Activity Season

Activity periods in terrestrial turtles vary with latitude, elevation, and rainfall patterns, with periods of inactivity occurring during winters and dry seasons (Auffenberg and Iverson 1979). Activity in *Terrapene carolina* conforms to this general pattern. In the northern parts of its range it enters hibernation in late October or November, whereas extreme southern populations may remain semi-active all year (Ernst and Barbour 1972, Dodd et al. 1994).

The *T. carolina* repatriated to Floyd Bennett Field were active, on average, from 21 April through 24 October, for an average activity season of 185 days (Table 11). Extreme individuals were observed basking on the surface at the entrance to a hibernaculum on warm afternoons as early as the first week of April or as late as the first week of November. Another population of Long Island *Terrapene* was generally active from May through October, with limited activity recorded as early as 8 April and as late as 15-22 November (Madden 1975). Based on radio-tagged individuals, the mean activity year in this population ran from 24 April through 6 November, a period of 196 days. In a Maryland population, the active year generally extended from 1 May through 31 October, a period of 184 days (Stickel and Bunck 1989). However, based on hibernation data, hibernation ended, on average, on 7 April and activity extended to 25 October, an activity year of 198 days (Stickel 1989). Contrasting with these results, which show a general agreement, are those of an Ohio population of _T. carolina_. In this population, hibernation generally ended in March and began from mid-October to mid-November. The average activity year was 222 days (Claussen et al. 1991).

While it is difficult to explain the longer activity season observed in the Ohio population, the concordance between the turtles at Floyd Bennett Field and those studied by Madden and Stickel indicates that the activity season of repatriated turtles was similar to that of other nearby populations not subjected to repatriation.

4.B.b. Types of Activity

Though data vary in their nature, they indicate that even during the activity season, terrestrial turtles spend much of their time resting (Stickel 1950, Legler 1960, Auffenberg and Iverson 1979, Wilson et al. 1994). In Florida _Gopherus polyphemus_, adult males were active (not in their burrow) for 18.5% of the available daylight hours over the course of a year (Auffenberg and Iverson 1979). Radio-tagged juveniles were active only 10% of the time, apparently in response to predation pressures or high temperatures (Wilson et al. 1994).

The activity pattern of FBF Terrapene generally conformed to that described by many authors (Reagan 1974, Madden 1975, Strang 1983, Stuart and Miller 1987, Dodd et al. 1994). In the spring and fall, animals tended to be active during the warmer middle hours of the day, whereas in the summer, activity was greater in the early morning hours. Summer rains stimulated activity, and individuals captured under these conditions usually showed evidence of feeding.

T. carolina on Floyd Bennett Field also spent most of their time resting, with a total of 84.2% of active season observations being of animals at rest at the surface, partially covered in a form, or dug into leaf litter (Table 12). In a Florida population of T. c. bauri, 75% of all captures involved animals at rest or under cover (Dodd et al. 1994). In this case, animals were captured through active search and did not have radios, so there is probably a sampling bias against resting animals, particularly those under cover. Complicating either technique is the possibility that in at least some cases, animals seemingly at rest on the surface were reacting to the researcher's approach.

With respect to repatriation, one behavior of particular interest is the ability to encounter members of the opposite sex for reproductive purposes. At Floyd Bennett Field, courtship or mating accounted for 0.48% of all observations and an additional 0.72% of observations involved close proximity between the sexes (less than 0.5 m apart). On Egmont Key in Florida, 0.15% of all observations involved mating (Dodd et al. 1994), whereas in Maryland, 2.67% of all observations involved mating (Stickel 1978).

The role of population density in rates of mating in _T. carolina_ was discussed by Mosimann (1958), who predicted a positive correlation between density and inter-sex encounters. Thus, the high incidence of mating in the Maryland population may be due to the high population density, 9.9 to 12.4 individuals/ha (Stickel 1950). However, on 180 ha Egmont Key, over 1100 individuals have been recorded, of which 84.7% (924) are adult (Dodd 1994, pers. comm.). Average adult density is minimally 5.13/ha, though the reported avoidance of certain habitats would increase the effective density. The low rate of mating observed here is less than density would suggest. Though few individuals in this population were observed mating, they were highly aggregated, often found sheltering or feeding in large groups under individual plants. The density and high proportion of juveniles in the population certainly indicate there is no lack of reproduction.

Density of box turtles on Floyd Bennett Field is difficult to accurately estimate, given that turtles were released over the course of four years, and were dispersing out from the release point. Thus, in reality, density varied over time and distance from the release point as animals were released and dispersed varying distances or died. Based only on individuals known to be alive in a given year, the mean number of individuals present during the period 1988 through 1993 was 119. Given that the minimum convex polygon of all radio-telemetry locations on Floyd Bennett Field has an area of 158.4 ha, a minimum estimate of mean density during this period is 0.75 individuals/ha. Since, within this polygon there were 21.8 ha (13.7%) of runway, plus 36.7 ha (26.9%) of extensive grassland that were avoided, the effective density is higher, somewhere between 0.87 and 1.19 individuals/ha. In another Long Island population, density was estimated at 3.71/ha (Madden 1975).

While the density of the repatriated Terrapene was considerably less than reported for these and other studies (Legler 1960, Doroff and Kieth 1991, Williams and Parker 1987, Dolbeer 1969, Schwartz and Schwartz 1974), the observations of mating and inter-sex proximity suggest that inability to find a mate is not a limiting factor. Taking into account that Terrapene possess the ability to store sperm for a few year (Ewing 1943), Mosimann (1958) suggested that populations of Terrapene could maintain themselves, in terms of mate finding, at densities as low as 0.62 individuals/ha. This estimate was based on probabilities of random encounter, without any special mechanisms for mate location. Considering that olfactory cues are used for mate finding in some lizards (Cooper and Vitt 1986) and snakes (Ford 1986), and that gopher tortoises use olfaction for courtship and territoriality (Owens et al. 1986, Allison et al. 1994), it is possible that olfaction also plays a role in mate finding in Terrapene. Such a mechanism would increase the rate of mating encounters and further enhance the species' ability to maintain reproductive output during periods of low population density. Thus, the low density of Terrapene on Floyd Bennett Field appears to be adequate for mate finding, a conclusion supported by the observations of matings that occurred during the course of the study.

4.B.c. Dispersal - Direction, Speed, and Distance

The ability of displaced box turtles (genus Terrapene) to home or show homeward orientation has been long known (Nichols 1917, Breder 1927). Studies of this phenomenon have been of two general types 1) experimental orientation trials, and 2) following movements in-situ of animals released at sites outside of (or at least believed to be outside of) their normal home range.

Gould (1957, 1959) conducted a series of experiments with individuals selected for their tendency to return in the approximate homeward direction (ca. 50% of individuals tested showed this tendency). The turtles were taken to release sites 0.5 to 9.0 km from home and followed for a period of 10 to 120 minutes following release. Releases occurred under sunny and cloudy skies. Homeward movements occurred only under sunny conditions. Gould concluded that these individuals were capable of homing (based on their tendency to move in a homeward direction) and that the sun was the cue utilized. Madden (1975) pointed out many problems with Gould's experimental approach however, and Gould's data alone should not be viewed as conclusive.

DeRosa and Taylor (1980) conducted orientation experiments in a terrestrial arena, 50 m in diameter. They found that test _T_. _c_. _carolina_, originating from 15 to 150 km away, showed a significant degree of homeward orientation on sunny days, but not on cloudy. Use of the sun, or other celestial cue was further demonstrated by phase-shifting turtles six hours. These oriented 90 degrees clockwise of home, as predicted (DeRosa and Taylor 1982), and demonstrate that _T_. _carolina_ utilize solar cues in conjunction with an internal biological clock for homing. In addition, Mathis and Moore (1988) demonstrated that _T_. _carolina_ are capable of magnetically-based compass orientation, and speculated that box turtles use magnetic information to establish a homeward direction and solar cues to maintain the course.

In reporting on experimental relocations, Nichols (1939b) concluded that overall, 89.5% of adult T. c. carolina studied in a Long Island, NY population showed some homing instinct. While most of these had been displaced less that 0.8 km, of 13 individuals displaced somewhat greater distances (1000 to 1400 m), 11 successfully homed (returned to locality where originally found). Lemkau (1970) displaced 14 T. c. carolina 0.6 to 2.0 km from home and followed their movements for an average of 44.6 days after release, during which time they moved, on average, 345 m. Thirteen headed in a homeward direction. Similarly, Williams and Parker (1987) documented the successful return of 13 individuals from distances up to 777 m.

In T. ornata, Metcalf and Metcalf (1970) documented a 20% return rate for individuals displaced up to 2.4 km. In a follow-up study, Metcalf and Metcalf (1978) documented successful homing after displacements ranging from 1.6 to 3.2 km, but noted that as distance of displacement increased, the ability to home successfully decreased. An individual taken from 80.5 km away and released in their study area remained there (Metcalf and Metcalf 1970). Schwartz and Schwartz (1974) relocated 40 T. c. triunguis from 0.4 to 201 km into their

22.3 ha study area. Of these, 17 were recaptured on the study area, though some of these recaptures were during the same or subsequent year, and could represent turtles in the process of returning home. Seven of the 40 however, were recaptured repeatedly three to eight years after transplanting, and had established normal home ranges. They all had been taken from distances of 1.7 to 3.4 km. The remaining 33 apparently left the study area, but since it was relatively small (22.3 ha), it is uncertain how far they ultimately dispersed after release, or in what direction.

In another Long Island, NY population of _T_. _c_. _carolina_, Madden (1975) conducted 40 experimental displacements (from 250 to 1,140 m) with 18 different individuals. Thirty eight resulted in successful homing. Posey (1979) found that nine of 10 _T_. _c_. _carolina_ displaced 500-900 m successfully homed. However, three individuals displaced from 1.6 to 8.0 km failed to show any homeward movement, and moved in a manner similar to those of an animal on its home range. Hall (1987) relocated nine _T_. _c_. _carolina_ a distance of 28 km. Two individuals subsequently had patterns of movement typical of individuals already resident, whereas most of the remaining seven dispersed from the release point in highly uni-directional routes unrelated to homeward orientation (Type II orientation). Post-release monitoring of these animals was conducted for ca. 1-2 weeks, during which time they had dispersed ca. 100-500 m. Gould (1957) also found evidence of Type II orientation in animals displaced 290 and 644 km.

Doroff and Keith (1990) conducted two experimental releases with T. ornata in south-central Wisconsin. One group of five was relocated 30 km and followed by radio-telemetry for ca. 5 weeks. During this period, none of the five appeared to disperse, though one died and another was lost track of. A second group from Nebraska (distance not reported), consisted of six individuals. One was lost track of and one of the remaining five remained at the site, moving up to 0.8 km from the release site before hibernating. The remaining four dispersed from the release site, with contact being lost at distances from release point ranging from 0.4 to 8.8 km. No data on directionality of post-release movements are provided.

While these studies collectively demonstrate that many T. carolina are capable of homing, and that solar and magnetic cues appear to be the likely mechanisms, they also show there is considerable individual variation in either the ability to successfully home or the tendency to attempt homing. Earlier works (Nichols 1939b, Metcalf and Metcalf 1970, 1978, Schwartz and Schwartz 1974) relied on subsequent recapture, rather than trailer devices or radio-telemetry, and may underestimate rates of successful homing. Since, in the early studies, nothing is known of routes taken nor distance travelled after release by the animals that did not successfully return home, there is no way of knowing if they attempted to home or if they established new home ranges.

For studies where post-release movements were followed, the evidence for homing in animals relocated relatively short distances (up to ca. 2 km) is very strong (Lemkau 1970, Madden 1975, Posey 1979). However, when relocated greater distances, the homing response appears to break down. Some individuals move about similarly to residents or show no inclination to disperse, whereas others disperse from the release site, but not in a significantly homeward orientation (Gould 1957, Posey 1979, Hall 1987, Doroff and Kieth 1990). While these results are pretty much in agreement among themselves, and consistent as well with anecdotal observations of long distance relocations (Nichols 1939b, Metcalf and Metcalf 1970, Schwartz and Schwartz 1974), what detracts from these studies and constrains their conclusions is their relatively short duration. Posey's lasted six weeks, Hall's was up to two weeks, and Doroff and Kieth radio-tracked for up to nearly six weeks. At FBF, several Terrapene remained within 100 m of the release point, and engaged in random movements for up to a few months before setting out on long distance, unidirectional moves. Madden (1975) noted that animals took up to 21 days to begin a homeward journey. These observations suggest that some of the results reported by Posey, Hall, Gould, and Doroff and

Kieth may have been different had they been extended over a longer time period.

Posey (1979) suggested there is a "critical distance", ca. 1.6 km, beyond which, relocated Terrapene will not attempt to home from. While the literature supports the idea that there is an inverse relationship between distance relocated and homing, it also indicates that Terrapene repatriated long distances often disperse from the release site. Since these studies did not extend for more than a few weeks and/or did not analyze homewardness of movements, it is impossible to conclude that some homing is not occurring. The fact that there also are many examples of individuals establishing new home ranges after long distance repatriations (Metcalf and Metcalf 1970, Schwartz and Schwartz 1974, Mathis and Moore 1988) demonstrates that not all individuals home or disperse. What is likely happening is that, as distance relocated or repatriated increases, the ability and tendency to home decreases, particularly beyond a few kilometers where there is little likelihood of prior familiarity with the release site.

Thus while arena tests have demonstrated the ability of Terrapene displaced 15-150 km to orient in a homeward direction (Derosa and Taylor 1980) they provide no insight into the persistence of homing over time or space. Animals actually displaced these distances appear to be more variable in their response, but studies to date have not collected adequate long-term data to answer questions on the extent and persistence of homing after long distance repatriation.

For T. carolina repatriated to Floyd Bennett Field, analysis of both 100 m and 200 m vanishing bearings indicate that there was significant clustering around the homeward bearing, and that the home bearing was within the 95% confidence interval of the mean. Thus for the pooled population of radio-tagged Terrapene, the hypothesis of homing can not be rejected. However, group by group analysis indicates that there is considerable variation in homing tendency. When tested as individual groups, pet0, wild0, and wild 15 were shown to have dispersed randomly. Only the pet15's dispersed non-randomly.

For some unknown reason, the pet15's were highly clustered in the homeward direction. This result is contrary to the a priori hypothesis that individuals taken from the wild and quickly released without on-site holding would be most likely to attempt homing. Pet15's, of course, represent the opposite extreme of this treatment. Distance repatriated is an unlikely explanation, considering that pet15's were, on average, repatriated the greatest distance of all four groups and that some studies show homing tendency to decrease with distance repatriated. This factor would suggest that pet15's would be least likely to home. Though there were significant between group differences in mean distances repatriated, it is hard to imagine that there is a biologically significant difference between being repatriated 60 versus 85 km.

Since all individuals were released at the same point, any local feature influences would be expected to operate on individuals of all categories. Releases were done contemporaneously, though not necessarily on the same dates for all groups. Practical constraints relating to the collection, transportation, and processing of turtles precluded this. However, since the mean times required to reach the 200 m radius ranged from 29.8 to 125.7 days (pet15 was 91.3) it seems unlikely that conditions at the time of release would exert much influence on the outcome. Sex also seems an unlikely explanation, since there were no significant between-group differences in sex ratios (p=0.91, Fisher Exact Test), nor were there significant differences attributable to sex in transformed 200 m vanishing bearings (Mardia-Watson Wheeler chi Square=1.4, df=2, p=0.5). Thus no satisfactory explanation other than random chance seems to exist for why the pet15's, as a group, differed from the others in their mean bearing and homeward orientation.

Though the significant homewardness of the overall vanishing bearings indicate that homing can not be rejected, this apparent homing is not conclusive evidence that homing actually did occur. The homeward orientation observed in the T. carolina repatriated to Floyd Bennett Field could also be a form of non-sense orientation (Matthews 1968) or the result of release site bias (Wallraff 1978). While the mechanisms and causes of these phenomena are not well understood, their existence has been demonstrated in many groups of birds. Thus any definitive conclusions regarding homing must be made cautiously. To demonstrate that these phenomena were not operating at Floyd Bennett Field would have required additional releases, involving animals collected from all compass directions, not just the animals collected from the east (ie. from Long Island). This would help determine if the Terrapene dispersed in a homeward direction, regardless of what direction home happened to be, or if there is some site-specific factor that resulted in a tendency towards dispersal to the east (which was home for the individuals released) regardless of where home happens to be. Such releases would have required animals collected from mainland New York and New Jersey, which was inconsistent with the goals of the repatriation program. Program goals required that, for zoogeographic and genetic reasons, only "local" animals (ie. from Long Island, NY), be repatriated.

The general tendency towards homing displayed by the repatriated Terrapene is consistent with most of the literature on this subject. For long distance repatriations, the results obtained here are intermediate between those of Hall (1987) who reported no significant homeward orientation, and the highly directed homeward response obtained by DeRosa and Taylor (1982) in their pen trails. While the Terrapene repatriated to Floyd Bennett Field appear to have homed, there was considerable variation in the homewardness of vanishing bearings. This greater degree of dispersion is seen in the relatively low values for vector length (r=0.234) and home component (hc=0.214) measured at the 200 m radius. Values obtained from the data of De Rosa and Taylor (1982) (r=0.642, hc=0.582) and from Lemkau (1970) (r=0.41, hc=0.362) indicate that the vanishing bearings in these studies were more highly clustered homeward.

Since the determination of whether a population of individuals has homed or not is based on the entire population, there is no way to statistically test an individual's homing performance. However, as an index of how close to and tightly clustered around the homeward bearing a population is, individuals were classified, based on their 200 m vanishing bearing, as being within 45 degrees of the home bearing (ie. from 315-045 degrees) or not. For the Terrapene repatriated to Floyd Bennett Field, 46% (24/52) were within 45 degrees of homeward whereas, in the case of DeRosa and Taylor (1980) 75% (18/24) were. These differences were significant (Fisher exact test p=0.03), further substantiating that the apparent homing shown by the Floyd Bennett Field Terrapene was relatively weak.

Homewardness, measured as a vanishing bearing, may not necessarily be related to the overall outcome of a repatriation. Direction of dispersal provides no information on the speed or distance dispersed, nor may it have any relationship to whether an individual establishes a home range or not. There was no significant difference in vanishing bearings between individuals that established home ranges versus those that dispersed (Mardia-Watson-Wheeler chi-square=2.7, df=2, p>0.1). Moreover, individuals that established home ranges were significantly oriented in the homeward direction (mean bearing=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 dispersed from the site were not significantly oriented (mean bearing=300.5, r=0.280, hc=0.142,, u=0.724, p>0.10) and did not home.

Another analysis of the relationship between homewardness and home range establishment was performed by comparing the fate of individuals whose vanishing bearings were within 45 degrees of home with those who were not. Of the 20 individuals in the first category, 16 established home ranges and four did not. Of the 18 individuals that did not orient to within 45 degrees of home, 9 established home ranges and 9 left the site. These frequencies did not differ significantly from random (Fisher exact test p=0.09), indicating that establishment of home range was not related to homewardness of dispersal.

There is some bias in these data, however, due to the location of the release point. Since the assumption was that homing would occur, animals had more room to the east (homeward) and south, and considerably less to the west and northwest (Figure 3). Animals that dispersed west and north-west had significantly less distance to travel before they ran out of room and moved off-site. Of the 13 individuals that left the site, four had moved westerly. The result of this bias however, would be to increase the number of individuals that had not oriented within 45 degrees of home leaving the site. Statistically, this could have led to erroneous conclusions of significant relationship between homewardness and home range establishment. However, in spite of this bias, such conclusions were not made. In addition, what is perhaps most significant is that, even among those individuals that dispersed most closely towards the home bearing, 80% of them established home ranges on Floyd Bennett Field. This demonstrates that even if repatriated Terrapene do home, most do not persist indefinitely in this behavior. They eventually establish new home ranges.

The values for time100 and time200 indicate there was tremendous individual variation in dispersal speeds. Many individuals reached the 100 m radius fairly quickly, ca. 39% in less than 10 days, and 75% had done so after 54 days. A somewhat similar pattern was seen for time200, though the time was greater and proportionately more individuals had above average times. Such variation in dispersal speed seems typical, as does the frequency distribution of dispersal times. Other Long Island Terrapene, relocated relatively short distances, took from 0 to 14 days to disperse beyond 50 m from the release point, with a mean of 2.2 days. Most (82%) had reached the 50 meter point within four days (Madden (1975). Data from Lemkau (1970) provide estimates of individual average dispersal speed ranging from 71 to 171 m/day. Williams and Parker (1987) also noted considerable variability in individual dispersal speeds, also after short distance relocations. Average daily rate of movement ranged from 10 to 421 m/day (mean 74.7).

Differences between time100 and time200 were significant (log likelihood ratio chi square=14.12, df=1, p=0.0002). These differences indicate that, in reaching the greater distance, the Terrapene were more spread out over time, probably because movements of some individuals had, by this point in time, shifted from linear dispersal to the more random patterns associated with movements on a home range. Some individuals still alive at the end of the study (ie. T313, T513) had yet to reach the 200 m point. These differences suggest that time100 is the better measure of initial dispersal speed.

Analysis of initial dispersal speed (time100) as a function of several possible explanatory variables shows a number of tendencies (Table 17). While not statistically significant, wild caught Terrapene tended to disperse from the release point more rapidly than pets, with wild0 being the most rapid. Compared to the other three groups (pet0, pet15, wild15), the consistently lower mean and quantile values of wild0 indicate that this group moved quickly from the release point, with most individuals closely spaced in time. This is consistent with the prediction that wild0 would be the group most likely to "take off" upon release.

The relationship of distance repatriated to time100 showed no significant linear relationship between distance and dispersal speed (r=0.004, p=0.97). A similar lack of correlation between dispersal speed and distance relocated was reported by Madden (1975). Considering that the animals in Madden's study were short distance relocations, and those in this study considerably longer distance, and both groups had very low correlation coefficients, it would seem that distance relocated has no influence on rate of dispersal.

No significant differences in dispersal speed were attributable to age or sex. However, no young age classes were tested, only young adult and middle aged adults. Individuals that dispersed homeward (within 45 degrees of home) took significantly longer to reach the 100 m radius (p=0.001), indicating that rapid initial dispersal is not related to homeward orientation. Hall (1987) also reported rapid (compared to this study), non-homeward uni-directional movement in <u>Terrapene</u> repatriated long distance (28 km). Speed of initial dispersal (time100) was found to be inversely related to the overall distance dispersed from the release point. Based on linear regression, r=0.28, p=0.04, and maxdist=-0.96 time 100 + 476.68. Though the low value of the correlation coefficient indicates a high degree of variation, the general trend is that initially fast moving individuals will disperse further from the release point than slow movers. This trend is corroborated by ranked correlation (Spearman correlation coefficient=-0.382, p=0.005). In addition, individuals that left the site reached both the 100 m and 200 m radii in significantly less time than individuals that established home ranges (Table 17).

Distance dispersed or maximum distance (measured as maximum straight-line distance from the release point) was quite variable ranging from 113 to 1295 m (mean 592.1, median 475). Though the data show a slight skewing of values towards the lower end of the range (Figures 14, 16), there is also a likely bias in these data against high values. Floyd Bennett Field is not part of a continuous landscape, across which animals could be easily tracked. Animals missing due to radio failure or leaving the site undoubtedly would have increased the values for maximum distance, had they been followed. Animals that dispersed shorter distances were (all other things being equal) less likely to be lost track of, and more likely to be recovered after radio failure.

Terrapene moving greater distances than recorded here have been reported. In experimental relocations of T. ornata, one group of five individuals had, over the course of three to six weeks, dispersed the following distances, 0.4, 0.8, 1.0, 7.0, 4.0, and 8.8 km (Doroff and Kieth 1990). Three transient T. c. triunguis were followed straight line distances of 10.0, 2.8, and 1.4 km, over periods of 15, 2, and 12 calendar months respectively (Kiester et al. 1982).

In spite of these limitations, data on maximum distance accurately reflect the fact many individuals did not disperse great distances, even after three to five years of continuous monitoring. Under more ideal circumstances, the data would probably show a greater maximum distance, and proportionately more individuals with high values.

Based on these analyses, a general model of the post-release behavior of Terrapene can be described. Though there is a high degree of individual variation, Terrapene disperse in a homeward direction. Individuals taken directly from the wild and released within a few days show no greater tendency to disperse homeward than individuals held a minimum of 15 days on or off site prior to release. Homewardness was not associated with rapid initial dispersal from the release point nor did it have any positive relationship to eventual establishment of a new home range. Individuals that left the site tended to be those showing rapid initial dispersal. Individuals that dispersed rapidly tended to ultimately disperse greater distances from the release point. The majority of individuals remained within a kilometer of the release point.

These conclusions indicate that while repatriated Terrapene appear to have a tendency to disperse homewardly, this dispersal does not persist indefinitely. Rather, most eventually establish home ranges within one kilometer of the release site. Moreover, variation in the speed of dispersal (for which no explanations were found) rather than homewardness appears to play a greater role in whether individuals established home ranges or left the site.

4.B.d. RESERVE SIZE

Reserve size is one of the most important issues in species conservation and has been the subject of extensive research and discussion (reviewed by Shafer 1990). For repatriated animals this issue is perhaps even more critical, since once released, they disperse from the release point into the adjacent habitats. Dispersal often incorporates homing, and distances travelled are often greater than movements undertaken by animals on their original home range (see for example Doroff and Kieth 1990). For repatriation to succeed, animals must remain on the release site (reserve) in sufficient numbers and density to reproduce.

In rural and wildland landscapes, many reserves are buffered by similar habitats and relatively compatible land use. Hence the actual area of habitat capable of supporting the repatriated population may be much larger than the administrative boundaries of the reserve which serves as the release site. However, as fragmentation and urbanization increase, these buffers are lost and effective reserve size will be reduced to that of the reserve alone and probably even further, due to edge effects (Lovejoy et al. 1986). For purposes of this discussion, a release site is considered an isolated patch of habitat, surrounded by other habitats and land use activities unfavorable to the survival and reproduction of the repatriated species. Departures from the release site are demographically equivalent to mortality.

In the case of the Terrapene repatriated to Floyd Bennett Field, data on maximum straight line distance from release point can be used to provide estimates of reserve size required to retain increasing proportions of repatriated individuals. Assuming a circular shape (since animals dispersed in all directions) and radius equal to the maximum distance, reserve size can be calculated. This indicates that, based on the maximum distance of 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 (Figure 50).

These estimates, which are conservative due to the bias towards short distance dispersed discussed above, suggest that reserves intended for repatriated T. carolina need to be a minimum of 300 hectares to reasonably retain most individuals. It is not, however, necessarily an estimate of reserve size needed for protection of an extant population. Few data exist on this question. Most studies of Terrapene were on small study areas that essentially sampled a portion of a population distributed over a much larger area, often in a fairly continuous landscape. While these studies provide good estimates of population density, they are less useful in providing estimates of the size of an entire population or the area supporting that population. One exception, however, is a population of T. c. bauri on Egmont Key, Florida, a 180 ha island. During a three year period, 124 juveniles and 687 adults were captured (Dodd et al. 1994) and follow up work has shown the population to be even larger (Dodd, pers. comm). The relatively high proportion of juveniles noted by Dodd et al. (1994), suggests that this population is quite viable. This example indicates that 180 ha is supporting a viable population. However, populations on true islands are confined (Mushinsky and McCoy 1994), and rates of loss to emigration into population sinks are probably much less than in habitat islands in fragmented landscapes. While far more work is needed to sample many populations and determine their area needs, these results suggest that populations of T. carolina will require at least 200 to 300 ha of habitat to maintain themselves over the long term.

4.B.e. GROWTH

Animals as long lived and slow growing as Terrapene make difficult subjects for in situ studies of growth, particularly since juveniles (the smallest, fastest growing and most definitively aged individuals) are difficult to find (Stickel 1978, Dodd et al. 1994). Consequently, there have been very few studies. These indicate that growth in Terrapene follows the general chelonian pattern of rapid initial growth that declines after sexual maturity, as described above under _Chrysemys_. Even among the oldest and largest individuals, growth is variable, ranging from slight to none, with growth eventually ceasing. However, growth in some juveniles may show pauses of a year, and in adults it may be intermittent, resuming after long pauses (Nichols 1939). Alternately, growth is sometimes so slow that it appears to have stopped (Stickel and Bunck 1989). Such small increments would tend to go unmeasured over periods of just a few years. Conclusions regarding termination of growth are essentially _post facto_, based on obtaining identical measurements over the course of decades (Stickel and Bunck 1989).

While the relatively short period of time and the predominance of adults, whose growth has largely been completed, make this a less than ideal study of growth, the results here on Floyd Bennett Field conform to the general pattern of chelonian growth. Both juveniles (age class 1) and young adults (age class 2) showed greater and more variable growth than the older adults. Further evidence of the reduced growth in age classes 3 and 4 is seen in the greater proportion of individuals that showed no growth, in spite of the longer mean time period between first and last measurements (Table 24).

Though the extant studies of growth in _T. c. carolina_ are hard to compare directly because of differing methodologies, they provide some useful comparisons. Nichols (1939a) presented average annual rates of growth of Long Island individuals, based on size categories of plastron length. Sexes were combined and all data were in inches. I converted to millimeters and used data on carapace and plastron length (sexes combined) from Table 1 of Stickel and Bunck (1989) to develop the simple relationship, Carapace Length=Plastron Length/0.95738. Using comparison with the size data for each of my four age groups, Nichols' size groups can be roughly equated to one of my four age groups (Table 24). Compared to Nichols' data, growth of Floyd Bennett Field juveniles was greater, though based on only three individuals. Growth of young adults was slightly greater, and that of older adults slightly less. Similarly, compared to Stickel's data, growth of Floyd Bennett Field juveniles (age class 1) was greater, but that of young adults (age class 2) less. However, the general pattern, as well as magnitude of growth rates are very similar between the three. Though there are some problems with direct comparison's with the growth data of Nichols (1939a) and Stickel and Bunck (1989), overall the growth rates of Terrapene repatriated to Floyd Bennett Field indicate that they are growing at rates comparable to viable, naturally occurring populations.

4.B.f. SURVIVAL AND MORTALITY

Patterns of survival in terrestrial turtles are similar to those of aquatic and marine forms, with mortality generally inversely related to age. Based on 16 populations representing eight species within two families, annualized survivorship of terrestrial turtles can be characterized as moderate but highly variable from egg deposition to hatching (mean ± 1 SD=42.8% ± 25.5), and very high with low variability for sub-adults and adults (93.4% ± 4.5% and 88.7% ± 6.1%) respectively (Iverson 1990). Data on hatchlings and juveniles are scarce. Within the genus Gopherus, estimates of survival from hatching to year one range from 5.8 to 54.5% and from one year to maturity they range from 12.5 to 96.0% (Germano 1994). In general, survival of sub-adults and adult terrestrial turtles are the highest of all chelonians (Iverson 1990).

Among the Terrapene, adult survival is also high. Adult survival in T. ornata varies, ranging from 81-96% in a Texas population (Blair 1975). Estimates from other populations are within this range; 83% in Kansas {calculated by Iverson (1990) from data of Metcalf and Metcalf (1985)}, and 81% in Wisconsin.

The most thoroughly studied populations are those of T. carolina. In a Maryland population of T. c. carolina, average annualized survival over a thirty year period was 93.4%. Adult male survival was slightly higher than female, 93.9% v. 92.8%, and survival of individuals initially marked when young (less than 20 years) was similar to that of adult males. Overall annualized mortality for each of the study's three decades ranged from 89.6 to 96.5% (Stickel 1978). Similar survival rates were reported in a 26 year study of an Indiana population of carolina. Annualized survival of males averaged 93.2% (range 86.0-97.7%) and females 93.4% (range 87.8-100%). While no differences in survival due to sex were reported, young males had the highest rate of survival. Young females had the lowest survival, perhaps due to dispersal from the study site (Williams and Parker 1987).

In a Missouri population of T. c. triunguis, annualized survival over a 26 year period was 89%. Differences between sexes were slight (89.6% for males v. 90.3% for females), and survival of young adults (86.4%) was less than that of older adults (92.3%) (Schwartz and Schwartz 1991). The lower survival of young appears to be the result of greater dispersal rather than actual mortality. Contrasting with these studies is that of Yahner (1974), which reported an overall annualized survival rate of 79.5%, with survival lower in young v. old, and female v. males. This is probably an underestimate. Animals captured and marked over the course of an entire activity year in 1968 by Dolbeer (1969) were searched for, over the course of a three month period in 1972.

Considering that some individual Terrapene are more retiring, plus seasonal shifts in home ranges and the role of favorable weather conditions in stimulating surface activity (and thus capture), it is likely that, had recapture effort been closer to that of the initial capture, the recapture (survival) rate would have been higher.

Survival of Terrapene repatriated to Floyd Bennett Field was considerably lower than that of those populations not subject to repatriation. However, certain patterns of variation, such as lower survival of young adults (age class 2), are consistent with the results of Willliams and Parker (1987) and Schwartz and Schwartz (1991). Though there were no significant between year differences in survival rates, survival was nearly always lowest the first two years following release, whereupon it increased and became less variable (Figures 24-33). This initial period of low survival is seen in all release-year cohorts (Figure 24) and suggests that mortality is operating primarily as a function of time since release.

In analyzing survival, it is useful to look at its converse, mortality. In the conservative approach taken here, as well as in most other studies, mortality in the demographic sense consists of a number of components; known mortality, dispersal, and animals whose fate was unknown. These components can be further sub-divided, with each sub-division characterized differently with respect to when it operates, and on which segments of the population it principally operates on.

In both radio-tagged individuals and individuals without radios, most of the animals that were classified as unknown fate at the conclusion of field work were already unaccounted for after the first year or two. The increase in percent unknown is relatively small after the first two years (Figures 32, 34). This suggests that the predominant cause of an animal being classified as fate unknown is one that operates principally in the first couple of years after release. Animals classified as fate unknown may have dispersed from the site, or may still be present, either dead or alive and due to a host of reasons, they or their remains, have not been recaptured.

Of these three possibilities, dispersal from the site probably accounts for most of the unknowns. This conclusion is based on the data, discussed above in the section on home range, that show most initial recaptures occurred within a few years of release (Figure 39). Animals not initially recaptured (alive or dead) within a few years of release are unlikely to be recovered, even after several additional seasons of effort. Based on animals released without radios, of 61 individuals initially recaptured within two years of release and available for recapture in subsequent years (ie. not dead at initial recapture), 34 (55.7%) were recaptured at least once in subsequent years (ie. outyear 3 and beyond). In contrast, 165 individuals were not recaptured in the first two years after release. Of these, only 36 (21.8%) were subsequently recaptured. These differences are significant (chi-square=22.41, p<0.001).

A similar phenomenon was reported by 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 and left the site. While the concept of transience is difficult to apply to the animals repatriated to Floyd Bennett Field, the similarity in the lack of recaptures, even after several years of study, supports the interpretation that most of the animals never recaptured have left the site. Further support of this interpretation is seen in 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. In the former case (Williams and Parker 1987), the dispersers tended to be female, whereas in the latter (Schwartz and Schwartz 1991) they tended to be males. Also, this pattern is similar to that reported in a repatriation of _G_. _polyphemus_. All of the 57.4% "mortality" that occurred in the two years following release was due to animals leaving the release site, and nearly all of this had occurred within a year of the initial release (Burke 1989). Finally, analysis of time100 data has shown that animals determined to have left the site tended to disperse most rapidly.

All these points, in total, indicate that most of the individuals classified as unknown fate have probably left the site, and that they did so within a couple of years of release. Records exist for animals leaving Floyd Bennett Field and being killed by vehicles or being found by passers-by as they moved beyond the boundaries of Floyd Bennett Field. There is also evidence that some left Floyd Bennett Field by entering the waters of Jamiaca Bay. Though not an "unknown", T355 crossed Mill Basin (ca. 150 m wide) twice. In addition, T334 and T512 were both lost after being tracked to cover near the water's edge, and T092 was captured afloat in Jamaica Bay in 1994. Though this may seem unusual for box turtles, there are several reports of box turtles entering into water and swimming, including a number from Long Island, NY involving coastal waters (Nichols 1917, 1939b, Culver 1915, Latham 1916, Overton 1916, Tyler 1979). There were also two instances of individuals being found at locations where the only reasonable explanation is that they were transported there by humans. One involved an individual recovered in Bay Ridge, Brooklyn, and the second an individual recovered on Staten Island.

While relatively rapid dispersal from Floyd Bennett Field probably accounts for most of the unknowns, some of these turtles are undoubtedly still present. Schwartz and Schwartz (1991) believed that most of their unknowns (categorized separately from transients), which represented 43% of their population, were undetected deaths, possibly during hibernation. Finding the remains of dead individuals can be very difficult, particularly if they died underground during winter, and/or in dense habitats. In addition, some individuals are likely still alive. For example, in 1995, T273 was recaptured for the first time, having been released in 1988. The area of Floyd Bennett Field known to be used by radio-tagged turtles consisted of 136.7 ha of habitat, much of it dense and impenetrable. Additional area beyond these bounds was also searched. These were also used by some individuals without radios, meaning that the area used by all repatriated turtles is even larger than the 136.7 ha used by radio-tagged individuals. By comparison, the size of other _T_. _carolina_ study areas are 9.3 ha (Yahner 1974), 11.8 ha (Stickel 1978), 22.2 ha (Schwartz and Schwartz 1991), and 72.9 ha (Williams and Parker 1987). Considering the amount of habitat that needed to be covered at Floyd Bennett Field relative to these other studies, it seems likely that the _Terrapene_ at Floyd Bennett Field eluded recapture at rates that exceed these other studies.

The second component of demographic mortality is actual or known mortality. Similar to the unknowns, most of the known mortality occurred within two years of release, though the magnitude of this pattern was less pronounced for mortality. For example, among the 1988 release-year cohort (Figure 26), 71% all recorded mortality had occurred by the end of outyear two, whereas 97% of all unknowns had occurred by this point. The pattern is seen in almost all cohorts and groupings (Figures 25-35). It suggests that mortality is also dominated by factors which operate greatest within the first couple of years, but the effect of these factors is moderated by other factors which operate independent of time since release.

Predominant causes of recorded mortality were winter kill, unknown causes, and pneumonia. Half of the individuals classified as unknown had been missing due to radio failures and were recovered as skeletal remains. Cause of death could not be ascertained, but presumably some of these individuals died from winter kill or pneumonia. Though difficult to quantify exactly, winter kill and pneumonia were the two largest identified sources of mortality.

Eight out of nine cases of winter kill occurred within the first two winters after release. This could suggest that individuals recently released into a new site were unable to find adequate hibernation habitat. However, five of these eight cases occurred in the second rather than the first winter.

Another factor affecting overwinter mortality is year-specific weather. The rate of winter mortality for the winter of 1989-90 was 38.5%, and this winter accounted for 56% of all recorded winter mortality. Of the five individuals that died over that winter, three had survived hibernation the previous winter.

Climatic data for the months of December, January, and February (the period when extremes of cold occur) during the six winters for which winter mortality data were collected show that December 1989 was unusually cold. It had the lowest monthly mean temperature during this period (-3.1° C) as well as the greatest deviation below long term mean (5.15°C). On sixteen days, the daily high was below freezing. On five of these days, all within a seven day period and including four in a row, it was below -5° C. Such a severe early cold snap, when overwintering turtles are still relatively shallow (Dolbeer 1971, Congdon et al. 1989, Claussen et al. 1991, this study) seems the most plausible explanation for the high mortality experienced in the winter of 1989-90.

Overwintering mortality is a variable, and often major source of mortality in populations of <u>Terrapene</u> not subject to repatriation (Carpenter 1957, Metcalf and Metcalf 1970, Schwartz and Schwartz 1974, Doroff and Kieth 1990, Claussen et al. 1991). Neill (1948) felt that cold was the most significant cause of mortality in Georgia Terrapene. This would argue against the importance of repatriation-related factors such as time since release, and support the idea that random patterns of severely cold weather are the major influence on overwintering mortality.

Most of the deaths from pneumonia (four out of five) occurred between the first and second year after release. Individuals involved had the creamy nasal discharges described by Evans (1983), and showed a long term general pattern of gradual weight loss prior to death. Transmission of diseases is a major concern in repatriations, with respiratory diseases of turtles being a particularly acute problem (Berry 1986, Dodd and Seigel 1991, Jacobson et al. 1995). The observations on the Terrapene repatriated to Floyd Bennett Field suggest that disease transmission during the collecting, transporting, and penning stages occurred, and that it took a couple of years to run its course. Thus, the 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% respectively) is best seen as the result of losses due to dispersal from the study site and losses due to pneumonia (both of which are greatest in this early period and then diminish), plus a random event, a severe cold snap in December of 1989. This event was within two years of the release of 81.1% (43/53) of all radio-tagged turtles, and accounted for 9.4% (5/53) of all the radio-tagged turtles released. Following these initial two years, survival of radio-tagged turtles increased, ranging from 79% to 89%.

While the annualized survival for the entire five year post-release period was 71%, even the annualized survival for the last three years of this period, 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, Willliams and Parker 1987). Clearly, the initial survival of the repatriated Terrapene was greatly reduced and, even after disease and dispersal had run their course, survival rates were less than in populations not subject to repatriation. While some of this difference is undoubtedly due to losing track of animals that are actually still alive, the lower survivorship of the repatriated individuals does seem real.

Relatively low rates of known survival seem to be typical of repatriation efforts, with most of the available data obtained from repatriation of G.agasizii and G. polyphemus (reviewed by Berry 1986, Diemer 1989). What complicates comparative use of these studies however, are differences in methods, duration, and size of release sites. In one repatriation of G. polyphemus to a 40 ha release site, survival to two years post-release was 42.6%. This corresponds to annualized survival of 65.5%. No actual mortality was reported and all losses were apparently from dispersal in the first year (Burke 1989). In another repatriation of G. polyphemus, mean survival time of repatriated turtles (22 months) was considerably less than that of residents (53 months). These differences are the result of repatriated turtles leaving the release site, most of which occurred in the first year. Seventy percent of repatriated turtles were never recaptured, compared to 45% of residents. After the first year, the remaining repatriated turtles actually had a slightly higher survival (Layne 1989). The results obtained for T. carolina at Floyd Bennett Field appear consistent in general with the results of these other repatriations, though dispersal from the release site was a less important factor, and disease and winter kill correspondingly more important.

4.B.g. Reproduction

Compared to the vast literature on reproductive output that exists for aquatic turtles, there are few comparable data on terrestrial species. Morafka (1994) attributed the lack of concentrated or synchronous nesting as a factor in the scarcity of data on the eggs and nests of Gopherus, and this is probably true also for Terrapene. The only way to non-destructively obtain unequivocal data on the various aspects of reproduction in Terrapene is to follow radio-tagged females closely through the nesting season, and X-ray them at the start, middle, and end. Given the expense and intensity of effort required, and the fact that until recently Terrapene were not considered a high priority or vulnerable species, this lack of attention is understandable.

Mean clutch size of FBF Terrapene (5.8, range 1 - 9) is greater than reported for T. ornata in Wisconsin (mean=3.5, Doroff and Kieth 1990) or Kansas (mean=4.7, range 2 - 8) (Legler 1960). Estimates of clutch size in T. carolina show even greater variation, both within and between populations, with values for FBF turtles intermediate. Ewing (1935) reported the mean was 3.6 (range 1 - 7) for turtles from near Washington, DC. For a sample from throughout Connecticut, mean clutch size was 6.7 (range 3 - 9) (Klemens 1993).

As discussed above for Chrysemys, total annual reproductive output of a population is the product of mean clutch size times mean fecundity (the mean number of clutches produced by adult females). Thus data on clutch size must be incorporated into estimates of total reproductive output. Complicating this task is a dearth of data and methodological differences among the few existing studies. Legler (1960) based his estimates on follicle counts, and determined that all females produced at least one clutch and a third of them produced a second. This gives a mean fecundity of 1.33 clutches/female and a mean annual reproductive output of 6.25 eggs/adult female. In contrast, Doroff and Kieth (1990), using radio-tracking *in situ* and X-rays, found no evidence of double clutching, a mean fecundity of 0.57, and a mean annual reproductive output of ca. 2 eggs/adult female. Ewing (1935) reported double clutching in some *T. carolina* individuals, and estimated the average number of eggs laid by a female in a single season to be 4.1 eggs. Based on an average clutch size of 3.6, mean fecundity would be 1.14 clutches/adult female. However, his data are for animals held in an outdoor pen. It is unclear if all or only some of the females laid eggs in a given year or if there was any supplemental feeding that could have influenced reproductive output. Mount (1985) states that Alabama *T. carolina* lay two to three clutches a year, but provides no detailed data. Oliver (1955) points out that *T. carolina* conforms to the general trend of clutch frequency decreasing with increasing latitude, with some Florida individuals laying up to four clutches annually, whereas individuals around New York normally producing one clutch.

Total annual reproductive output in FBF *T. carolina* was 2.74 eggs/adult female {mean fecundity (0.47 clutches/female) times mean clutch (5.68 eggs/clutch) = 2.74 eggs/female}. This value exceeds the estimate of Doroff and Kieth (1990) for free ranging T. ornata (ca. 2 eggs/female), but is less than the estimates of Legler (1960) or Ewing (1935), 6.25 and 4.1 eggs/female respectively.

It is possible that estimates of mean fecundity based on field study of free ranging populations are conservative, because of the difficulty of ensuring that an adequate sample of females are monitored across the entire potential nesting season. Klemens (1993) reported that Connecticut Terrapene nested mostly in mid-June, but listed an unusually early date for a gravid female as 19 May. Around Washington, DC, nesting dates ranged from 28 May through 14 July, with nearly half of all nests laid in July (Ewing 1933, 1935). Similarly, in North Carolina, gravid females were found beginning in May, and half of all records were during July (Stuart and Miller 1987). Nesting dates recorded for another Long Island, NY population ranged from 11 June 11 to 5 July, with most occurring in the last half of June (Madden 1975).

In this study, in 1993, turtles were X-rayed on 10 June 1993 and 25 June 1993. At each weekly recapture, palping was done whenever possible. There were no cases of negative X-rays on 10 June for animals that had previously palped positively, nor were there any instances of individuals palping positively after a negative X-ray on 25 June. This suggests that the X-rays on these two dates may have recorded all clutches, though it overlooks the fact that, due to the hinged plastron, female *Terrapene* are often impossible to palp in the field. In the mid-May to mid-July period of 1993, 61% of attempts to palp females were unsuccessful. Thus the possibility exists that some early or late clutches went undetected. However, since they represent extreme cases of low frequency, they probably do not heavily influence estimates of the mean.

All things considered, the estimated mean fecundity rate of 47% is best thought of as a minimum, though it is unlikely that it is too far off. It is much closer to the 57% mean fecundity reported by Doroff and Kieth (1990) for *T. ornata*, using similar methods and an intensity of monitoring at least equal to mine than it is to the estimates of Legler (1960) and Ewing (1935), based on follicle counts and captive specimens respectively.

The relatively low annual reproductive output of *T. carolina* at FBF may be attributable to a number of factors. Lack of opportunities for mating or poor habitat quality, with limited energy available for egg production are two possibilities, though the data on inter-sex encounters and growth do not seem to support these explanations. Another possibility is that annual reproductive output in *T. carolina* is inherently less.

Given the species' relatively greater age at maturity and longevity, this explanation is consistent with the inverse relationship between annual reproductive output and age at maturity and longevity demonstrated by Iverson (1992). Moreover the available data on longevity in the genus Terrapene, though not as geographically extensive as would be desirable, does show T. c. carolina to have the greatest survivorship and longevity (Williams and Parker 1987). Thus the lower annual reproductive output of FBF T. c. carolina, compared to other populations of Terrapene, may be due to the inter-related effects of specific and sub-specific differences in longevity and latitude, rather than due to effects relating to repatriation or the release site.

Data on individual patterns of annual reproductive effort in Terrapene are scarce. Whereas the work of Legler (1960) and Ewing (1935) imply that all adult females nest at least once every year, that of Doroff and Kieth (1991) does not. Though their sample size is small, of nine individuals with two consecutive year's data, four nested both years, three nested in only one year, and two individuals did not nest at all. For the Terrapene at FBF, based on 11 instances where there are data for two consecutive years, two nested in both years, five nested in only one of the two, and four did not nest at all (Table 30). This pattern is quite similar to that described by Doroff and Kieth (1990), though the greater number of nonnesters reflects the lower mean fecundity of the FBF Terrapene.

The timing of reproduction in the Terrapene at Floyd Bennett Field shows that the period when gravid females were present spanned from early June to early July, with most records during the last three weeks of June. Similarly, estimates of nesting dates show nesting concentrated in the last half of June. These dates are comparable to other nearby populations of T. carolina (Madden 1975, Klemens 1993), though they do not extend as far into July as reported for Washington, DC (Ewing 1933, 1935) or North Carolina (Stuart and Miller 1987). This difference is likely due to the fact that southerly populations of turtles tend to have less restricted nesting periods (Moll 1979, Iverson 1992).

The ten records of young turtles indicate that successful nesting and hatchling survival is occurring, though there are no data on rates. The concentration of records in the most recent years (Table 31) reflects the process whereby offspring produced in the early years of the project reach the age and size where their behavior shifts and they become more readily observed, as well as the increased ability to find turtles by using a dog. During the years when a dog was used (1993-1995), five of the eight young turtles recorded were found by the dog.

Overall, the reproductive data indicate that the repatriated Terrapene on Floyd Bennett Field are encountering mates and producing eggs and offspring that are surviving beyond the hatchling stage. Comparisons with non-repatriated populations are difficult due to minimal data on fecundity rates in other Terrapene populations, and lack of data on survival and recruitment in the repatriated (FBF) population. However, the results suggest that reproductive output is consistent with that of non-repatriated Terrapene, and in conjunction with the increasing numbers of young recorded, suggest that there is a growing population of FBF-native Terrapene.

4.B.h. HOME RANGE

4.B.h.1. Establishment

Establishment of new home ranges at the release site is one of the first in the sequence of events necessary for repatriation efforts to succeed. Data on rates of home range establishment or "settling behavior" (Berry 1986) are few, and so far, of limited utility in determinations of overall repatriation success. Since repatriated animals are more likely to disperse beyond the bounds of small sites, settlings rates can be influenced by size of release sites. Often study or release sites are not ecologically isolated or discrete, but rather a sample or subset of a larger, more continuous landscape. Moreover, monitoring data may also be limited in duration (eg. due to limited effort or radio failure), and conclusions about settling behavior not indicative of the ultimate outcome. However, some of this limitation is simply due to a lack of sufficient elapsed time. With the passage of time, conclusions concerning repatriation success can be based on long term data, and then, correlations between success and settling rates can be analyzed.

The establishment of a new home range by repatriated Terrapene has been extensively documented. However, all these examples lack methodologies that address the above issues. Nichols (1939b) noted that two individuals for which "return would have been impractical, remained near where liberated". Of 40 T. c. triunguis repatriated into a 22.3 ha Missouri site, seven (17.5%) established new home ranges. All seven had been collected from locations from 1.6 to 3.2 km away (Schwartz and Schwartz 1974). In a population of Kansas T. o. ornata, 5% of repatriated individuals, collected from peripheral areas up to 2.4 km away, appeared to establish themselves on the 3.3 ha study area (Metcalf and Metcalf 1970). These studies, particularly the latter, are limited because, for many individuals, the distances involved are relatively short distance displacements to contiguous portions of the landscape, rather than long distance repatriation. In addition, the release sites are relatively small.

In Gopherus agassizii, settling rates ranging from 30-50% have been reported (Berry 1986), though some of the data these rates are based on are relatively short term (e.g. a month). Settling rates in G. polyphemus appear to vary according to release area size and habitat quality. One hundred percent settling was reported on a 259 ha site (Fucigna and Nickerson 1989). On a 40 ha site, 43% of individuals remained after two years (Burke 1989) and Stout (1989) reported settling rates of 58% and 55% for two separate relocation efforts at similar sized sites. In a 52.6 ha, high habitat quality site, 50% of individuals settled, whereas at a 16.2 ha site, only 29% of individuals settled within 0.5 km of the release point (Godley 1989). A circle of radius 0.5 km comprises 78.5 ha. This last point illustrates the role of habitat quality in dispersal distance and settling rates, as well as the problems (both programmatic and methodological) of small release sites.

The 47% settling rate in Terrapene repatriated to Floyd Bennett Field is higher than reported for other populations of Terrapene, though those other populations are probably underestimates. It is comparable to that found in most studies of Gopherus. However, it is considerably less than the 100% rate for G. polyphemus released on a 259 ha site. Since Floyd Bennett Field is twice that size (575 ha), all things being equal, a comparable settling rate would be expected. Several factors are probably responsible for this difference.

1. Though a large site, the release point was not located centrally. The shortest distance from release point to the site boundary was ca. 300 m, and some individuals left the site after travelling distances less than 500 m.

2. *Terrapene* do not reside in and base their activities around burrows as do *Gopherus*. There are many reports of transients and repatriated individuals traveling long distances. *Terrapene* appear to be a more mobile species and hence require a larger area to disperse into.

3. Many individuals at Floyd Bennett Field that failed to establish home ranges included those that died, mostly due to pneumonia and winter kill. These problems were not reported in any of the work on *G. polyphemus*.

Overall, the settling rate for the *Terrapene* repatriated to Floyd Bennett Field corresponds closely to the recommendations for repatriating *G. polyphemus*. Landers (1981) found that only half the released animals will establish themselves at the release site. Undoubtedly, the settling rate of *T. carolina* at Floyd Bennett Field could have been improved by using a more centralized release point, and by taking better precautions to reduce spread of disease.

4.B.h.2. Home Range Size

Home range size has been studied in many populations of Terrapene. Though these studies vary in their duration, sample sizes, and method of calculating home range, they generally have reached similar conclusions regarding the magnitude of home range size, home range stability, and the relationships of sex and age to home range size.

In T. c. carolina, mean home range estimates based on a range length diameter and circular shape are 0.43 ha (Dolbeer 1969), 2.19 ha (Strang 1983), and 3.17 ha (Nichols 1939). Based on one year and long term (3-26 years) data respectively, mean home range estimates are 1.00 ha and 2.30 ha for males, and 1.68 ha and 2.44 ha for females (Williams and Parker 1987).

Using the 95% bivariate normal method, Stickel (1989) estimated the mean female home range to be 1.13 ha and males 1.20. Home range size was not significantly increased by inclusion of long term data. Similarly, Madden (1975) estimated a mean home range of 6.96 ha, with no differences due to sex.

In a population of T. c. triunguis, using the minimum rectangle method, no sexual differences were found in the size of long term home ranges. However, the long term home range 5.1 ha, based on up to 19 years of data, was much larger than the estimate based on the first six years, 2.1 ha (Schwartz et al. 1984).

Whereas Schwartz et al. (1984) and Williams and Parker (1987) report that long term home ranges are larger than those of a single year, Stickel (1989) found no significant differences between single year and long term home ranges. In the case of Schwartz et al. and Stickel, these differences seem to be due to differences in vegetation and successional processes. The site where large differences were found by Schwartz et al. had old fields succeeding into woodlands, and the greater long term home range is likely due to turtles expanding their ranges into the recently developed woody habitat (Schwartz et al. 1989).

The general conclusions supported by these works, as well as those on _T_. _ornata_ (Legler 1960, Doroff and Kieth 1990) is that home range size is not significantly affected by sex, juveniles and sub-adults have smaller home ranges than adults, and adult home ranges are stable in size and location over time. Variation in home range size at both the inter and intra-population level appear attributable to habitat quality and diversity, with diverse, high quality habitat correlated with small home ranges (Madden 1975, Stickel 1989).

For the _Terrapene_ repatriated to Floyd Bennett Field, estimates of total range are highly variable (Table 32), reflecting the great variability in dispersal distances. Total range estimates also demonstrate the relatively large area that repatriated _Terrapene_ utilize in the course of dispersing from the release point. That most of this area is traveled across rather than "utilized" for food and cover is seen in two ways. The 95% harmonic mean estimate, which is better at identifying core areas actually used, had a mean value of 8.50 ha, as opposed to the mean 95% bivariate normal estimate of 22.58. The difference between these two means is significant (t=-4.183, df=128, p=0.000). Secondly, 95% bivariate normal home ranges averaged 35% of total range (range 35 to 115%) and 95% harmonic mean home ranges averaged 44% of total range (range 3% to 142%). Clearly the total area that individuals range across is far larger than actually used in terms of meeting typical resource needs but represents a need none-the-less. That need is for sufficient space to allow for the waning of homing or type II movements.

Home range size of _T_. _carolina_ at Floyd Bennett Field exceeded all other published accounts, though methodological differences make some comparisons less useful. The mean 95% bivariate normal home range, 9.77 ha, is slightly larger than the 6.96 ha reported for another Long Island population (Madden 1975), and considerably larger than in Maryland bottomland forest. There males averaged 1.20 ha and females 1.13 (Stickel 1989). Differences between the home range size on Long Island versus Maryland have been 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 higher quality habitat than drier forest or more open habitats.

Compared to the study sites of Madden and Stickel, as well as the others cited above, Floyd Bennett Field is a lower quality habitat. Due to its recent creation, shrub thicket and woodland habitat is limited in quantity (compared to the other sites) and patchily distributed. Moving from patch to patch, separated by less preferred open grassy habitats (Reagan 1974), results in larger estimates of 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 the fact that harmonic mean estimates better reflect actual area used, and tend to exclude non-utilized areas, such as, in this case, the patches of unused habitat in between the woody habitats. Even the 95% harmonic mean estimate however, reflects the lower habitat quality of Floyd Bennett Field, exceeding Madden's 1.76 ha estimate of actual utilized home range.

Though home range size was greater for FBF Terrapene, 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). Though females had larger home ranges than males, due in part to inclusion of females that nested, differences between the sexes were not significant. When gravid females were excluded, the between sex differences were much less. 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 Kieth 1990).

The larger home ranges of gravid females, compared to those not gravid, is consistent with the reports of Williams and Parker (1987) and Stickel (1989) that nesting forays often take females to areas beyond their "normal" home range. Thus while there may not be any inter-sex differences in the amount of area required to meet energy requirements and other general needs, larger areas may be needed to provide specialized requirements such as nesting habitat. While it may simply be a matter of defining "normal", nesting is certainly a critical activity, and nesting areas an important habitat element, especially where establishing and maintaining viable populations is concerned.

The extent to which nesting requirements increase the spatial requirements (and thus estimates of home range size) of Terrapene is likely dependent on the animal's habitat. Stickel (1989) indicated that females extended their home ranges by leaving the bottomland forest to nest in drier and warmer upland sites. On the other hand, Madden (1975) concluded that most females nested at sites that could be considered part of their home range. In this case, habitats were more mesic and more diverse than those of Stickel, and the home range size reported by Madden is over five times that reported by Stickel. Given the larger home range size and greater heterogeneity of habitat at the Long Island site studied by Madden, there would be less need for a nesting foray beyond the home range. This last point would suggest that at Floyd Bennett Field, with its relatively high degree of habitat diversity, 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), suggesting that prior experience plays a role in determining the destination of nesting movements. The repatriated turtles lack this prior experience at Floyd Bennett Field, and presumably have to search more extensively for suitable nesting sites.

4.B.h.3. Home Range Stability

Though Nichols (1939b) reported that some individuals may shift home ranges over the years, most adult Terrapene tend to have stable home ranges (Legler 1960, Schwartz et al. 1984, Doroff and Kieth 1990). Yahner (1974) reported that 88.8% of T. c. carolina did not significantly shift home range from 1968-69 to 1972. During a 26 year study, 10.2% of females and 15.2% of the males shifted home range (Williams and Parker 1987). Only one of eight individuals (12.5%) studied by Madden (1975) showed a significant home range shift (ca. 200 m). 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 17-124 m) was still relatively small.

Inter-year comparisons of home range geographic centers indicate that home ranges of Terrapene at Floyd Bennett Field are less stable than in other populations. Only 40% of comparisons were non-significant. Though more inter-year shifting is occurring at Floyd Bennett Field, the magnitude of the shifts (mean distance between geographic centers= 99.7 m, range 16.5 to 202.9) is similar to the results of Madden (1975) and Stickel (1989). The greater amount of inter-year shifting at Floyd Bennett Field is likely due to the patchier nature of the habitat there, but may also suggest that home range locations are not as firmly established as in non-repatriated populations. However, the magnitude of the shifts are relatively small scale, and indicate that once an individual establishes a home range, it is likely to remain on the site thereafter.

4.B.h.4 Stability of Hibernacula

Fidelity to hibernation sites has been documented in populations of T. ornata (Metcalf and Metcalf 1979, Doroff and Kieth 1990), T. c. triunguis (Carpenter 1957), and T. c. carolina (Madden 1975, Stickel 1989, Claussen et al. 1991). While these works demonstrate that individuals often return to the same hibernation site, they also indicate that this behavior is quite variable, both between and within individuals. In the most detailed of these works, Carpenter (1957) concluded that there was "great variation in the tendency and/or non-tendency of individuals to return to hibernacula they had previously occupied". Collectively, these works indicate that some individuals consistently use the same hibernation site, others generally do but occasionally skip a year (and hibernate elsewhere), whereas others are less predictable.

Carpenter (1957) reported the following frequencies of inter-hibernacula distances; less than 10 m - 40 instances, from 10 to 61 m - 36 instances, from 61 to 152 m - 20 instances, from 152 to 365 m - 3 instances, and greater than 365 m - one instance. This frequency distribution is similar to that shown by Floyd Bennett Field *Terrapene* (Figure 48), though the mean distance reported by Carpenter (1957) was 49.4 m, compared to the mean inter-hibernacula distance of 97.6 m on Floyd Bennett Field. The site studied by Carpenter (1957) however, was nearly all woodland, and as a habitat was probably much less patchy than Floyd Bennett Field.

Overall, the patterns of hibernation site fidelity in the *T. c. carolina* repatriated to Floyd Bennett Field are similar to those seen in naturally-occurring populations. These results provide additional evidence that repatriated individuals are familiarizing themselves with habitat features at the repatriation site, and using this information to engage in patterns of behavior similar to animals that were not subject to repatriation.

4.B.i. Habitat Relationships

Terrapene carolina is well known to be a woodland species (Cahn 1937) that occurs in both moist bottomland forest (Stickel 1978) as well as drier upland forest (Strang 1983). *T. carolina* seems to prefer (and reach higher densities in) moist over dry forest habitats (Carpenter 1957, Madden 1975, Stickel 1978, Williams and Parker 1987), though there are some reports of no preferences between lowland and upland forest (Strang 1983). Though a woodland species, a number of descriptions of good habitat mention the presence of open patches in the overstory (Schwartz and Schwartz 1974, Stickel 1978) and well developed understory and herbaceous ground layer (Cahn 1937, Dolbeer 1969). The patchiness provides important micro-habitat for basking and a diversity of foods (Stickel 1950, Schwartz and Schwartz 1974). The importance of the edge provided by patchiness was further demonstrated by Madden (1975), who found that turtles favored the ecotonal edges between forests and field and brushy habitats.

Use of habitat by T. carolina on Floyd Bennett Field generally reflected the affinity of this species for habitats dominated by woody vegetation and avoidance of open habitats. In this particular case, mature woodland habitat was not available, and the next closest thing, emerging woodlands and shrub thickets were selected. However, the fact that nearly half (19 of 40) of the individuals used habitat in proportion to its availability indicates that there is considerable variation in habitat use between individuals, as well as a certain plasticity in habitat selection. While open habitats (lawn and grassland-herbaceous) were generally avoided, this avoidance was least in gravid females during nesting season, reflecting the well established pattern of gravid females seeking out open habitats for nesting purposes.

Based on the pooled data, Phragmites-dominated habitats, created by wetland filling and generally felt to be of low value to native wildlife in the northeastern United States (Jones and Lehman 1986) was avoided. Yet it was preferred by seven of the 21 individuals that did not use habitat randomly and overall only 12 of 40 individuals avoided this habitat type. Those individuals showing a preference for Phragmites appear to be substituting this habitat type for woody habitat. As a hibernation habitat its use was proportionate to availability. These data suggest that Phragmites does have value as habitat for Terrapene, though certainly no more than provided by native shrub and woodland habitats.

Seasonal variation in habitat use by Terrapene appears to be driven by two basic factors. The first is limited to gravid females and reflects the movement of these individuals into open habitats for the purpose of nesting. Such shifts have been noted by Williams and Parker (1987) and documented quantitatively by Doroff and Kieth (1990). The second factor is climatic, specifically seasonal changes in temperature and humidity that influence habitat shifts as Terrapene move in response to shifting gradients of optimal temperature and humidity. This was demonstrated quantitatively by Reagan

(1974), who noted a seasonal shift in habitat utilization from grasslands in late spring and early fall to forested areas in summer, early spring, and late fall in T. c. triunguis. Activity in grasslands coincided with moderate temperatures and high moisture. At other seasons, wooded habitats were used to avoid temperature extremes and maintain high humidity. Similar results were also reported by Madden (1975) and Doroff and Kieth (1990).

Data on seasonal patterns of habitat use by T. carolina on Floyd Bennett Field are equivocal. While statistically, there were no significant differences in seasonal habitat use, some of the seasonal use patterns described above are weakly seen. For example, greatest use of open habitats (lawn and grassland/herbaceous) was by gravid females during the nesting season. During this period, 30.5% of all observations of gravid females occurred in open habitat, as opposed to 20.5% for non-gravid females and 6.2% for males. During the month of June (peak nesting season), use of open habitats by gravid females was 35.2%, compared to 20.0% and 9.6% for non-gravid females and males respectively. The only evidence of a seasonal pattern of habitat use similar to that described by Reagan (1974) is seen in the monthly use of habitat by females. These individuals showed a preference for woody habitat and a corresponding avoidance of open habitats in the early spring (April-May) and late fall (October-November) (Table 42).

Complicating the analysis of habitat use patterns on Floyd Bennett Field is the highly interspersed patchiness of the habitat. Most of the habitat there is within 25 m of another habitat type and thus, for all practical purposes, the site is largely an eco-tone of woody, herbaceous, and Phragmites-dominated habitat. In another study of Long Island Terrapene, Madden (1975) found a preference for forest-field and forest-brush ecotones, and avoidance of deep forest, forest-grass, and grass. In Madden’s study, grass was similar to field except it was regularly mowed, and his "field" is comparable to my grassland/herbaceous.

The patchiness of habitats at Floyd Bennett Field, and the ability to easily move from open to enclosed habitat, makes it possible for animals to follow gradients of temperature and humidity without undertaking long distance movements deep into a specific habitat. This diminishes the importance of fine tuning habitat selection. In addition, the relatively young habitats of Floyd Bennett Field do not provide as broad a range of habitat conditions as would be found at sites where woodland development is much older. In other words, differences between habitats at Floyd Bennett Field may not be as great as elsewhere, and thus there is a lesser degree of habitat choice available. Combined, these factors have resulted in habitat use patterns that are generally consistent (given the habitats available) with other populations of T. c. carolina, though not as well defined, particularly with respect to seasonal patterns.

4.B.j. CONCLUSIONS RE: REPATRIATION OF BOX TURTLES TO FLOYD BENNETT FIELD

Data collected over a seven year period demonstrate that T. carolina repatriated to Floyd Bennett Field tended to disperse in a homeward direction, though as individuals they were extremely variable. Age, sex, prior history, or on-site treatment were not important factors in that variation. Due to repatriation program constraints however, homing could not be conclusively demonstrated. Individuals varied in the speed of dispersal from the release point, and those with rapid dispersal were more likely to disperse beyond the site's boundary. Most individuals did not persist in homeward directed dispersal, but rather eventually established home ranges. Most home ranges were established within a kilometer of the release point, but some individuals established home ranges at greater distances. Based on the assumption of circular shape, and a central release point, release sites for T. carolina need to be at least 300 ha in order to retain most individuals.

Growth varied between individuals, and showed the typical inverse relationship to age. Rates of growth for repatriated individuals were comparable to those of non-repatriated populations.

Though good comparative data are limited, rates of reproductive output appear to be consistent with that of comparable populations of individuals not subjected to repatriation. Individuals are able to find each other for reproductive purposes, though the need for a large release site results in a relatively low population density, creating potential problems with mate finding. Within three years of the first releases young were being recorded and increasing numbers of juveniles recorded in the latter years of the study suggest that successful reproduction is being sustained.

Survival of repatriated Terrapene was relatively low, particularly during the first two years. Dispersal from the release site, winter kill, and pneumonia were the predominant causes of death. Patterns of habitat use were similar to those of non-repatriated T. carolina, with woody dominated habitats preferred and open, herbaceous habitats avoided. Overall, Phragmites-dominated habitats were used in proportion to their availability, but several individuals showed a preference for this habitat type. Home range sizes on Floyd Bennett Field were greater than reported elsewhere, likely in response to the patchiness of the woody habitats. Females that were known to be gravid had larger home ranges, and used grassland-dominated habitats more frequently.

Overall, these results suggest that the T. carolina repatriated to Floyd Bennett Field have been able to successfully establish themselves in sufficient numbers to begin the process of establishing a viable population. This apparent success has come at the cost of high initial losses due to disease and off-site dispersal. It is too soon for any long term determination of success or failure. However, considering that survival rates of remaining individuals have stabilized, home ranges have been established, growth and successful reproduction are occurring, juveniles are being recorded in increasing numbers, and woody habitat is increasing due to successional processes, it would appear that prospects for long term success are encouraging. Thus results so far should be viewed with cautious optimism.

In a similar program, conducted at the nearby Jamaica Bay Wildlife Refuge, 208 adult T. carolina were repatriated during the period 1980-1986. In 1995, a fire burned 32.4 ha of this site, providing a sample of 31 individuals, all but one dead, and most killed by the fire. Twenty four of these 31 were unmarked individuals less than 15 years of age, meaning they were the offspring of the repatriated individuals. The high proportion of young individuals in this population indicates that this repatriation effort will likely succeed, setbacks from fire notwithstanding. The similarity between Floyd Bennett Field and Jamaica Bay Wildlife Refuge in their histories, habitats, and current management activities suggest that a similar course of events is likely on Floyd Bennett Field.

Chapter 5. COMPARATIVE PROBLEMS IN REPATRIATION OF TURTLES

C. picta and *T. carolina* possess different life history traits which have profound implications on the ability to repatriate these species, as well as monitor repatriation efforts.

The aquatic *C. picta* resides in a far more discretely defined and less abundant habitat than the terrestrial *T. carolina*. *C. picta* are essentially concentrated in ponds and wetlands, and through their habit of conspicuous basking, areas of concentration can be identified. Using baited traps they are easily collected. *T. carolina*, on the other hand, is more uniformly distributed across a larger landscape. It is not concentrated and can not be readily trapped. It is cryptic in color and frequents dense habitats where movement and lines of sight of researchers are restricted. While both species have annual activity periods that are roughly comparable, daily *Terrapene* activity is constrained by temperature and humidity. These environmental parameters are far less variable on a daily basis in an aquatic environment. While the use of trained dogs increases the ability to capture *Terrapene*, in general this difference in habitats results in *Chrysemys* being far easier to capture than *Terrapene*. This in turn makes *Chrysemys* a less difficult and less expensive species to attempt repatriation with, as well as to monitor. In addition, whereas populations of *Chrysemys* can be repatriated into and supported by relatively small ponds and adjacent uplands, as small perhaps as only a few hectares, populations of Terrapene appear to require at least a few hundred hectares.

Though both Chrysemys and Terrapene are relatively long-lived, longevity in Terrapene is clearly greater. As discussed above under reproduction, annual reproductive effort is inversely correlated with longevity. For females at Floyd Bennett Field, average annual reproductive output was 11.73 eggs/year in Chrysemys and 2.74 eggs/year in Terrapene. This difference results in faster population turnover and population growth in Chrysemys, compared to Terrapene. In repatriation, these differences mean that Chrysemys is better able to respond quickly to release into an unexploited niche. From a programmatic perspective, these differences necessitate different time frames for monitoring repatriation results. Given the longevity and low reproductive output in Terrapene, monitoring will have to be conducted over a longer time period, or at least conducted at points in time since repatriation that are greater than in Chrysemys. Dodd and Seigel (1991) recommended that repatriations of tortoises be monitored for a minimum of 20+ years. Continuous monitoring for this length of time would be very expensive, but would provide valuable data on the fate of repatriated animals and, if the program is successful, provide documentation of that fact. Alternately, periodic monitoring, conducted every five or ten years, provides data useful to evaluating the status of the repatriated population, but does not provide the detailed data of continuous monitoring. The data on repatriated Terrapene at Jamaica Bay Wildlife Refuge, reported above, in this case conducted opportunistically, demonstrate the kinds of information obtainable by this approach. While periodic monitoring will help keep programmatic costs down, the fact still remains that the greater longevity of Terrapene will require a longer term commitment to monitoring.

Though difficult to quantify precisely, these differences between Chrysemys and Terrapene in life histories mean that opportunities for repatriation of Terrapene would be far fewer, due to minimum area needs that are two orders of magnitude greater, and implementation and monitoring costs that are at least one order of magnitude greater and require a longer term commitment.

Chapter 6. RECOMMENDATIONS FOR REPATRIATION OF PAINTED AND BOX TURTLES

Repatriation is an action with the potential for profound biological and ecological consequences (both positive and negative) and should only be undertaken after extensive review. The problems of repatriation, and criteria that must be met for such an action to be valid as a conservation strategy, as well as likely to succeed, have been reviewed by Kushlan (1980), Burke (1991), Reinert (1991), Dodd and Seigel (1991), and Fellers and Drost (1995). Assuming that the numerous and strict criteria provided by the above sources are met, and repatriation is to be undertaken, the following additional points or recommendations can be made, based on the results of the work at Floyd Bennett Field.

6.A. Painted Turtles

1. Relatively small ponds can support populations of _C_. _picta_, provided they have abundant aquatic vegetation and do not freeze solid. Adjacent uplands must provide open habitat for nesting. Habitat complexes as small as a few hectare appear sufficient. These habitats can be naturally-occurring or human-created.

2. Most C. picta repatriated long distances do not home persistently. They appear to distribute themselves among the available aquatic habitat. The amount, nature, and juxtaposition of suitable aquatic habitats at the release site will largely influence where repatriated individuals end up after release. Post-release monitoring programs should sample all available aquatic habitats, not only the specific one that animals are released into.

3. Following marking and processing, animals can be released directly. Pens did not serve any useful purpose and may actually diminish survival.

4. Initial, intensive monitoring should be conducted for the first few years following repatriation. If these short term efforts provide evidence of repatriation success, follow up monitoring after an additional five to ten years should be undertaken to provide longer term results.

6.B. Eastern Box Turtle

1. While as a statistical population the repatriated Terrapene dispersed homewards, individuals dispersed in all directions and, for planning purposes, release points should be located as centrally within the release site as possible.

2. The greatest loss of individuals appears to be from dispersal beyond the boundaries of the release site. Thus larger sites will have better rates of retaining individuals as they disperse from the release point prior to settling into a home range. Release sites should be a minimum of 300 ha, preferably 500 ha, of fair to high quality habitat, ie. shrubland and woodland-dominated habitat.

3. The second greatest manageable loss was to disease, in this case pneumonia. Individuals with pneumonia, or appearing unhealthy in any way, should not be collected for repatriation. Animals should be transported, marked, processed, and released as quickly as possible, and as isolated from each other as possible. Animals with any overt signs that suggest it is unhealthy should never be held with any others, and should not be released.

4. Holding animals in pens prior to release does not appear to serve any useful purpose and may help spread disease.

5. Initial intensive monitoring should be carried out for the first three to five years after release. All animals should be marked with tags and by shell notching. Radio-telemetry should also be employed to follow post-release dispersal, with particular attention to distances dispersed and rates of loss due to animals moving off the site. If this short-term

monitoring provides evidence of repatriation success, periodic monitoring at five to ten year intervals for the next 20 to 30 years should be conducted to provide an appraisal of success over the long term.

Table 1. Sampling effort in monitoring repatriated *C. picta* and *T. carolina* (Total Hrs=hours spent by human workers, Dog Hrs=hours spent by Labrador Retriever "Gus", RT=radiotracking, AS=active search)

1a. *C. picta* trapping effort

Year	Dates	# Trapdays	Annual Total	
1991	3/28-5/2	175		
1991	7/24-8/2	82		
1991	9/16-9/23	98	355	
1992	5/26-6/2	102		
1992	9/14-9/25	220	322	
1993	5/21-5/27	138		
1993	6/4-6/11	168		
1993	6/17-6/26	207		
1993	9/15-10/11	546	1059	
Total				1736

1b. *T. carolina* Field Hours

Year	Total Hrs	Hours RT	Hours AS	Dog Hrs
1988	693	343	350	0
1989	506	306	200	0
1990	238	188	50	0
1991	136	136	100	0
1992	935	485	450	0
1993	819	350	469	424
1994	72	0	72	63
1995	65	0	65	65
Total	3464	1808	1691	487

Table 2. Summary of *T. carolina* repatriated to Floyd Bennett Field.

Totals by Age, Year, and Sex

	1987 Release		1988 Release		1989 Release		1990 Release		
	Male	Female	Male	Female	Male	Female	Male	Female	Total
Age 1		1				2		5	8
Age 2	20	16	11	35	12	17	7	7	125
Age 3	12	9	46	22	32	29	22	11	183
Age 4		4	2	6	3	3		1	19
Total	32	30	59	63	47	51	29	24	335

Totals by Age and Sex

Age	Male	Female	Total
Age 1		8	8
Age 2	50	75	125
Age 3	112	71	183
Age 4	5	14	19
Total	167	168	335

Totals by Sex and Year

Sex	1987	1988	1989	1990	Total
immature	1		2	5	8
Male	32	59	47	29	167
Female	29	63	49	19	160
Total	62	122	98	53	335

Table 3. Annual survival rates of C. picta repatriated to Floyd Bennett Field in 1990. Grouped by age, sex, and treatment in holding pen.

Group/Treatment	# Alive 1990	# Alive 1991	# Alive1992	# Alive1993
all individuals	55	49	43	42
adult male=all males	26	22	17	17
all females	29	27	26	25
adult females	19	17	16	16
juv females=all juv	10	10	10	9
all adults	45	39	33	33
no pen	22	21	19	18
escaped pen	12	12	10	10
held 10 days	21	16	14	14

Group/Treatment	Survival 90 to 91	Survival 91 to 92	Survival 92 to 93	Survival 90 to 93
all individuals	89.1%	87.8%	97.7%	76.4%
adult male=all males	84.6%	77.3%	100.0%	65.4%
all females	93.1%	96.3%	96.2%	86.2%
adult females	89.5%	94.1%	100.0%	84.2%
juv females=all juv	100.0%	100.0%	90.0%	90.0%
all adults	86.7%	84.6%	100.0%	73.3%
no pen	95.5%	90.5%	94.7%	81.8%
escaped pen	100.0%	83.3%	100.0%	83.3%
held 10 days	76.2%	87.5%	100.0%	66.7%

Table 4. Analysis of survival in C. picta repatriated to Floyd Bennett Field. Survival from release in 1990 through 1993.

SINGLE FACTOR ANALYSIS

Variable	Chi-square	p	df
Age (females only)	0.02	0.75<p<0.9	1
Sex	2.24	0.1<p<0.25	1
pen trmt	1.78	0.25<p<0.5	2
held 10 days	1.01	0.25<p<0.5	1

MULTI-FACTOR ANALYSIS

LIFEREG PROCEDURE

Variable	Chi-Square	p	df
Intercept	10.11	0.00	1
Sex	1.18	0.28	1
Age	0.28	0.60	1
Treatment	0.83	0.36	1

PROPORTIONAL HAZARDS REGRESSION

Main effects with interactions

Variable	Chi-square	p	df
sex	0.06	0.80	1
age	0.04	0.84	1
trmt	0.00	0.99	1
sex*age			0
sex*trmt	0.97	0.32	1
age*trmt	0.00	0.99	1

Main effects, no interactions

Variable	Chi-square	p	df
sex	0.90	0.34	1
age	0.27	0.61	1
trmt	0.69	0.41	1

Table 5. Annual plastron length growth (mm) in male *C. picta* repatriated to Floyd Bennett Field. SD=standard deviation.

1991 Growth

Plastron Length	n	Mean Growth (mm)	SD	Range	Mean % GRO
80-89 mm	3	6.7	4.51	2 to 11	7.9
90-99	3	5.3	2.52	3 to 8	5.9
100-109	6	2.8	1.83	0 to 4	2.7
110-119	3	3.0	1.00	2 to 4	2.6
120-129	1	0.0	0.00	0	0.0
130-139	2	2.5	0.71	2 to 3	1.9

1992 Growth

Plastron Length	n	Mean Growth (mm)	SD	Range	Mean % GRO
80-89 mm	1	2.0	0.00	0	2.3
90-99	3	3.3	2.31	2 to 6	3.6
100-109	6	0.8	0.98	0 to 2	0.8
110-119	3	1.3	0.58	1 to 2	1.2
120-129	2	0.0	0.00	0	0.0
130-139	2	0.0	0.00	0	0.0

1993 Growth

Plastron Length	n	MeanGrowth (mm)	SD	Range	Mean % GRO
90-99 mm	3	0.3	0.58	0 to 1	0.4
100-109	5	0.6	0.55	0 to 1	0.6
110-119	3	0.0	0.00	0	0.0
120-129	2	0.0	0.00	0	0.0
130-139	1	0.0	0.00	0	0.0

Mean Annual Growth 1990 through 1993

Plastron Length	n	MeanGrowth (mm)	SD	Range	Mean % GRO
80-89 mm	4	5.5	4.36	2 to 11	6.5
90-99	9	3.0	2.78	0 to 8	3.3
100-109	17	1.5	1.59	0 to 4	1.4
110-119	9	1.4	1.42	0 to 4	1.2
120-129	5	0.0	0.00	0	0.0
130-139	5	1.0	1.41	0 to 3	0.8

Table 6. Annual plastron length growth (mm) in female C. picta repatriated to Floyd Bennett Field. SD=standard deviation.

1991Growth

Plastron Length	n	Mean Growth (mm)	SD	Range	Mean % GRO
60-69 mm	1	13.0	0.00	0	18.8
70-79	0				
80-89	3	14.0	1.73	13 to16	16.9
90-99	3	10.0	6.93	2 to 14	10.3
100-109	3	8.7	2.08	7 to 11	8.4
110-119	2	10.5	3.54	8 to 13	8.7
120-129	1	1.0	0.00	0	0.7
130-139	6	3.5	2.35	0 to 6	2.7
140-149	6	1.3	1.75	0 to 4	0.9
150-159	0				
160-169	1	0.0	0.00	0	0.0

1992 Growth

Plastron Length	n	Mean Growth (mm)	SD	Range	Mean % GRO
80-89 mm	1	12.0	0.00	0	14.6
90-99	3	5.7	3.21	2 to 8	5.8
100-109	1	3.0	0.00	0	3.0
110-119	4	2.8	0.96	2 to 4	2.4
120-129	1	0.0	0.00	0	0.0
130-139	7	1.3	0.49	1 to 2	1.0
140-149	7	0.7	0.49	0 to 1	0.5
160-169	1	1.0	0.00	0	0.6

1993 Growth

Plastron Length	n	MeanGrowth (mm)	SD	Range	Mean % GRO
100-109 mm	4	2.3	1.71	0 to 4	2.2
110-119	3	1.7	0.58	1 to 2	1.4
120-129	1	3.0	0.00	0	2.5
130-139	6	0.7	1.21	0 to 3	0.5
140-149	3	0.0	0.00	0	0.0
150-159	1	2.0	0.00	0	1.3

Mean Annual Growth 1990 through 1993

Plastron Length	n	MeanGrowth (mm)	SD	Range	Mean % GRO
60-69 mm	1	13.0	0.00	0	18.8
70-79	0				
80-89	4	13.5	1.73	12 to 16	16.4
90-99	6	7.8	5.38	2 to 14	8.1
100-109	8	4.8	3.62	0 to 11	4.6
110-119	9	4.1	3.92	2 to 13	3.5
120-129	3	1.3	1.53	0 to 3	1.1
130-139	19	1.8	1.87	0 to 6	1.4
140-149	16	0.8	1.17	0 to 4	0.6
150-159	1	2.0	0.00	0	1.3
160-169	2	0.5	0.71	0 to 1	0.3

Table 7. Total rainfall and deviation from "normal" at JFK Airport, Queens, NY in C. picta growth season (May through August) during period of study. Data from National Weather Service.

Year	Amount (cm)	Deviation from "Normal" (cm)
1991	41.07	5.41
1992	43.48	7.82
1993	19.28	-17.96

Table 8. Reproductive output of C. picta in 1992 and 1993. Raw and summary data on clutch size, plastron length (PL) in spring 1993, number of clutches produced in 1993 and total number of eggs in 1993.

ID	1992 Clutch	1993 Clutch 1	1993 Clutch2	PLSpr93	#Clutches93	total eggs 93
0044	0	0	0	112	0	0
2002	0	0	0	120	0	0
7000H	0	0	0	120	0	0
7400	0	0	0	121	0	0
0420	0	6	0	125	1	6
0040H	0	7	0	131	1	7
0012	0	7	0	134	1	7
1002	0	6	0	134	1	6
CG	5	8	7	135	2	15
0110	0	9	7	137	2	16
0001D	0	10	0	139	1	10
7200	7	7	8	140	2	15
0010H	0	8	6	142	2	14
0210	5	0	0	142	0	0
0047	8	9	0	144	1	9
2000H	8	8	5	144	2	13
0700D	0	10	3	145	2	13
1100	0	8	0	146	1	8
1400	0	9	8	151	2	17
0020H	9	10	7	163	2	17
4060	0	no data	no data	no data	no data	no data

SUMMARY		
	1992	1993
adult females X-rayed	21	20
number gravid	6	15
%gravid	29%	75%
number w/1 clutch	na	7
number w/2 clutches	na	8
mean clutch all	7.00	7.52
mean clutch 1	na	8.13
mean clutch 2	na	6.38

Table 9. Mean clutch size in C. picta. Shown are means for 1992, all 1993 clutches, and first and second clutches in 1993.

All 1992 Clutches		All 1993 Clutches	
n	6	n	23
Mean	7.0	Mean	7.5
Standard Error	0.68	Standard Error	0.35
Minimum	5	Minimum	3
Maximum	9	Maximum	10

1993 - First Clutch		1993 Second Clutch	
n	15	n	8
Mean	8.1	Mean	6.4
Standard Error	0.35	Standard Error	0.60
Range	6 to 10	Range	3 to 8

Table 10. Plastron length of femal C. picta producing zero, one, and two clutches of eggs in 1993.

	0 Clutch	1 Clutch	2 Clutch
	112	125	135
	120	131	137
	120	134	140
	121	134	142
	142	139	144
		144	145
		146	151
			163
n	5	7	8
mean	123.0	136.1	144.6
SD	11.22	7.38	8.93

Table 11. Mean activity season and hibernation period for T. carolina at Floyd Bennett Field. Mean dates for initiation and cessation of activity in the spring and fall respectively. Based on radio-tagged turtles.

Activity Year	Begin	n	End	n	Length (days)
1988	NA	NA	27-Oct	19	NA
1989	19-Apr	13	28-Oct	13	192
1990	22-Apr	7	28-Oct	15	189
1991	18-Apr	17	22-Oct	10	187
1992	23-Apr	10	16-Oct	14	176
1993	21-Apr	14	20-Oct	18	182
Mean	21-Apr		24-Oct		185

Hibernation	begin	end	Length	
1988-89	27-Oct	19-Apr	174	
1989-90	28-Oct	22-Apr	176	
1990-91	28-Oct	18-Apr	172	
1991-92	22-Oct	23-Apr	184	
1992-93	16-Oct	21-Apr	187	
1993-94	20-Oct	21-Apr	183	end estimated from means
1994-95	24-Oct	21-Apr	179	all estimated from means

Table 12. Observed activity of radio-tagged T. carolina repatriated to Floyd Bennett Field. Active season records only.

ACTIVITY		# Obs	%
resting on surface		1075	51.3%
resting in a form		469	22.4%
completely covered		222	10.6%
walking		193	9.2%
basking		74	3.5%
soaking		14	0.7%
feeding		13	0.6%
swiming		1	0.0%
drinking		1	0.0%
defecating		1	0.0%
courtship		2	0.0%
mating		8	0.4%
with or near	male/male	8	0.4%
	female/female	1	0.0%
	male/female	15	0.7%
	Total Obs	2097	100%

Table 13. Mean homeward direction (degrees magnetic) of T. carolina repatriated to Floyd Bennett Field.

Group	Mean	vector length (r)	n
Pet0	85.2	0.993	14
Pet15	85.6	0.998	11
Wild0	77.7	0.972	15
Wild15	80.4	0.975	12

Table 14. Mean vanishing bearings, vector length (r), and analysis of vanishing bearings (Actual vanishing bearings, in degrees magnetic). ns=not significant at p=0.05 level.

100 Meter Radius

						Mardia-Watson-Wheeler Chi-Square					
Group	Mean	r	n	Rayleigh Test		Pet15	Wild0	Wild15	all 4 group	all wild	all pen 15
Pet0	43.7	0.195	14	p=0.60	Pet0 vs.	p=0.01	ns	ns			
Pet15	56.0	0.867	11	p<0.001	Pet15 vs		p=0.01	ns			
Wild0	328.7	0.175	15	p=0.64	Wild0 vs			ns			
Wild15	95.8	0.197	12	p=0.63	all 4 group				ns		
					all pet vs					ns	
all pet	53.3	0.489	25	p=0.00	all pen 0						p=0.05
all wild	26.2	0.083	27	p=0.84							
all pen 0	7.0	0.147	29	p=0.50							
all pen 15	63.6	0.498	23	p=0.00							
all inds	49.2	0.274	52	p=0.02							

200 Meter Radius

						Mardia-Watson-Wheeler Chi-Square					
Group	Mean	r	n	Rayleigh Test		Pet15	Wild0	Wild15	all 4 group	all wild	all pen 15
Pet0	53.7	0.251	14	p=0.42	Pet0 vs.	ns	ns	ns			
Pet15	64.5	0.807	11	p<0.001	Pet15 vs		p=0.02	ns			
Wild0	286.4	0.133	15	p=0.77	Wild0 vs			ns			
Wild15	116.4	0.246	12	p=0.49	all 4 group				ns		
					all pet vs					ns	
all pet	61.5	0.494	25	p=0.00	all pen 0						ns
all wild	135.6	0.039	27	p>0.90							
all pen 0	19.3	0.096	29	p=0.74							
all pen 15	76.7	0.476	23	p=0.00							
all inds	66.0	0.244	52	p=0.05							

Table 15. Mean vanishing bearings (transformed), vector length (r), and analysis of vanishing bearings (transformed to home=0 degrees magnetic).

100 meter radius

							Mardia-Watson-Wheeler Chi-Square					
	Mean	r	HomeComponent	n	V Test (U=)		Pet15	Wild0	Wild15	all 4 groups	all wild	all pen 15
Pet0	317.8	0.218	0.161	14	0.85	Pet0 vs.	p=0.015	ns	ns			
Pet15	330.6	0.852	0.742	11	3.48****	Pet15 vs		p=.004	ns			
Wild0	242.5	0.175	-0.081	15	-0.44	Wild0 vs			ns			
Wild15	357.8	0.129	0.129	12	0.63	all 4 groups				ns		
						all pet vs					ns	
all pet	327.5	0.495	0.417	25	2.95**	all pen 0						p=0.029
all wild	277.9	0.090	0.012	27	0.09							
all pen 0	283.4	0.155	0.036	29	0.27							
all pen 15	334.4	0.468	0.422	23	2.86**							
all inds	320.0	0.270	0.207	52	2.11*							

200 meter radius

							Mardia-Watson-Wheeler Chi-Square					
	Mean	r	HomeComponent	n	V Test (U=)		Pet15	Wild0	Wild15	all 4 groups	all wild	all pen 15
Pet0	326.1	0.278	0.231	14	1.22	Pet0 vs.	ns	ns	ns			
Pet15	338.1	0.799	0.741	11	3.48****	Pet15 vs		p=.004	ns			
Wild0	200.7	0.147	-0.138	15	-0.76	Wild0 vs			ns			
Wild15	35.2	0.185	0.151	12	0.74	all 4 groups				ns		
						all pet vs					p=0.048	
all pet	334.4	0.505	0.455	25	3.22***	all pen 0						ns
all wild	116.9	0.021	-0.010	27	-0.07							
all pen 0	291.5	0.109	0.040	29	0.31							
all pen 15	348.6	0.442	0.433	23	2.94**							
all inds	336.0	0.234	0.214	52	2.18*							

ns=not significant at the p=0.05 level. *,**,***, and ****=significant at the 0.05, 0.01, 0.001, and 0.00001 level respectively.

Table 16. Mean vanishing bearings (transformed) and 95% confidence intervals of mean bearings for *T. carolina* repatriated to Floyd Bennett Field. *=home bearing (360 degrees) within the 95% confidence bearing of mean.

100 m Radius						
		95% Interval				
Group	MeanBearing	LowLimit	UpLimit	r	n	deviation
Pet0	317.8			0.218	14	off chart
Pet15	330.6	307.6	353.6	0.852	11	23
Wild0	242.5			0.175	15	off chart
Wild15	357.8			0.129	12	off chart
all pet	327.5*	293.5	361.5	0.495	25	34
all wild	277.9			0.09	27	offchart
all pen 0	283.4			0.155	29	off chart
all pen 15	334.4*	297.4	371.4	0.468	23	37
all inds	320*	277	363	0.27	52	43

200 m Radius						
		95%	Interval			
Group	MeanBearing	LowLimit	UpLimit	r	n	deviation
Pet0	326.1			0.278	14	off chart
Pet15	338.1*	312.1	364.1	0.799	11	26
Wild0	200.7			0.147	15	off chart
Wild15	35.2			0.185	12	off chart
all pet	334.4*	301.4	367.4	0.505	25	33
all wild	116.9			0.021	27	off chart
all pen 0	291.5			0.109	29	off chart
all pen 15	348.6*	308.6	388.6	0.442	23	40
all inds	336*	280	392	0.234	52	56

Table 17. Speed of dispersal in *T. carolina*. Mean and quantile values (in days) of time 100 and time 200 and comparative analysis of relationship to sex, age, pre-release treatment and post-release dispersal and fate. SE=standard error.

Time 100 (days)	n	25%Quant	50%Quant	75%Quant	Mean	SE	Likelihood Ratio Test		
							Chi-Square	df	p
Pet 0	14	4	30	55	85.4	39.50			
Pet 15	11	6	32	54	72.6	40.11			
Wild 0	15	5	9	47	24.4	7.10			
Wild 15	12	13.5	33.5	104	59.3	18.96	1.110	3	0.775
All Inds	52	5	29	54	73.6	18.44			
all pets	25	6	32	55	80.9	28.84			
all wild	27	5	21	54	46.8	11.79	0.815	1	0.367
held 0 day	29	5	21	55	71.9	25.45			
held 15 day	23	8	32	54	70.0	24.33	0.127	1	0.721
male	30	6	33	70	94.2	28.21			
female	22	5	20.5	38	52.4	22.52	3.699	1	0.054
age 2	17	6	22	47	43.2	13.45			
age 3	35	5	31	55	78.3	23.14	0.293	1	0.589
left site	13	3	6	29	16.0	4.88			
estabHR	25	9	31	54	94.3	30.61	15.369	1	0.000
homeward	22	6	31.5	175	114.6	37.02			
not homeward	30	5	22	41	36.4	8.20	11.210	1	0.000

Time 200 (days)	n	25%Quant	50%Quant	75%Quant	Mean	SE	Likelihood Ratio Test		
							Chi-Square	df	p
Pet 0	14	54	101	255	125.7	29.45			
Pet 15	11	34	72	131	91.3	21.85			
Wild 0	15	9	21	59	29.9	6.33			
Wild 15	12	19	70	186	124.4	39.45	0.169	3	0.169
All Inds	52	14	66	178	116.9	19.77			
all pets	25	34	84	184	113.1	19.80			
all wild	27	14	35	178	108.6	28.80	4.189	1	0.041
held 0 day	29	13	58	149	96.0	20.25			
held 15 day	23	24	72	184	120.5	27.61	0.318	1	0.573
male	30	24	72	186	110.2	19.46			
female	22	13	58	145	92.6	26.30	1.715	1	0.190
age 2	17	29	70	149	87.7	17.65			
age 3	35	14	59	186	121.7	25.81	1.209	1	0.272
left site	13	10	59	60	8.1				
estabHR	25	14	58	186	28.9		8.146	1	0.004
homeward	24	14	70	186	119.7	28.11			
not homeward	30	21	58	178	81.6	14.92	0.704	1	0.401

Table 18. Data for Pet0 T. carolina, showing straight line distance from release point (in meters) over the course of the study. ActvTime=Activity Time, in days.

Pet0

Actv Time	T018	T020	T075	T089	T320	T323	T331	T356	T419	T457	T505	T510	T513	T563
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	11	70	108	14	3	127	125	28	68	72	36	19	11	16
2	17	70	108	16	3	221	148	26						
3	19	85	116	10	2	221	157	15	31	44	41	17		18
5					9	311			106	82				
7	29	108	125	9	9	392	138	29	140	82	44	25	12	17
14	74	95	120	11	33	407	344	16			54	54	13	17
21	60	158	180	63	33	538		26			65	60	111	73
28	79	286	155		32	561		16		95	106	27	50	67
42	175	321	168		30	549		138		120	166	30	54	77
56	143	317			36	551		132		314	167	68	63	87
70	180	434			30	796		90		204	147	56	43	214
84	190				23	853		47		276	133	57	42	445
112	187				40	912		41			127	272	66	562
140					47	698		47			118	236	75	625
168					95			117			243	345		883
196					115			108			354	365		869
224								112			161			867
252												372		867
280														
308						769						291		
336						781						294		
364	313					628							56	
392						581							124	
420						805		692					121	
448						841		611					115	
476						816		656						
504								735						
532						594		738						
560						486		729						
588					131	839								
616						844							39	
644						862							111	
672	234					833		808					90	
700	194					861		749					80	
728	195					834		739					43	
756	227					853		842			318			
784	201					834		632						
812	213					857		778						
840	266					798		649						
868						819		800						
896								789						
924								821						
952								767						
980								762						
1008								863						

Table 19. Data for Pet 15 T. carolina showing straight line distance from release point (in meters) over the course of the study. ActvTime=Activity Time, in days.

Pet15

Actv Time	T284	T299	T301	T313	T314	T332	T349	T350	T376	T380	T389	T535
0	0	0	0	0	0	0	0	0	0	0	0	0
1	21	17	4	9	29	9	18	79		0	6	10
2	13	17	7	6	23	43	14	84		0	7	
3	74	25	6	8	49	12	21	111	1	0	58	
5	138	45								2	58	36
7	210	29	110	53	112	12	68	204	1		55	
14	235	43		10		77	62	497	47		60	69
21	314	79		47			9				53	62
28	244	37		7		33	71		38		43	
42	236	139		84		458	63		43		81	163
56	327	169		78		464	144		38		95	163
70				82		484			38			217
84				63		598			37		293	213
112					173	569			41		295	269
140				60		584			260		317	264
168		178		39		589					317	206
196	320	210		17		467					270	259
224		226		58		567					259	200
252				99		576					288	
280				65		641					358	214
308				76	176						309	216
336				59							251	
364				98							263	
392				103							339	
420				30								
448				68								
476				113								
504				91				643			342	
532				88							301	
560				99							334	
588				98							310	
616				90							354	
644				89							349	
672				99							295	
700				102							273	
728				76							319	
756				93							251	
784				100							251	
812				74							341	
840				52							331	
868				57							322	
896				112							290	
924				103							265	
952				69							214	
980				76							256	
1008											277	
1036											342	

Table 20. Data for Wild0 T. carolina showing straight line distance from release point (in meters) over the course of the study. ActvTime=Active Time, in days.

Wild0

Actv	T253	T261	T303	T304	T308	T316	T324	T334	T343	T365	T370	T400	T425	T502	T520
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	27	12	9	6	84	27	9	133	26	28	31	17	88		
2	19	44		8			10		26	29	31	24	52	37	88
3	20		118	8	84	29	58	242	19	31	31	41			226
5	19	44	118	8	86	20	114	347	17	97	35	161			
7	25			8	86	25	226	369	40	276	33	106	70		
14	20	467		21	81	71	229	560	219	695	42	230	93	262	139
21	104	475		37	80	84		612	361	785	42	209	98		
28	19	408		41	73	96	239	609	230	664	38	250		293	376
42	58	414		50		55	238		91	947	42	270	276	293	386
56		419		31	129	242	228	644	54	915	71	314	276	373	389
70		419			310	176	243		57	912	86		312	529	
84		419			495	176	246		41		82		361		390
112		439				179			79		70	62	912	820	141
140	62	416				65			32		32	39	875	689	45
168	56								87		24	23	787	671	61
196	45								547		125	236	790	867	
224	31					123					110	214	737	820	87
252	118					130						27	690	878	
280	31					109						17	523	832	91
308	49											91	830	840	
336	59											36	826	847	
364	55											38		848	
392												17		838	
420												27		864	
448												87			
476												162			
504												160			
532												160			
560												160			
588												112			
616		184										366			
644		349										283			
672		201										302			
700		158										303			
728		261										183			
756		259										161			
784		261													
812		235													
840		194													
868		227													
896		151													
924									1120	1237					
952									1238						
980									1294						
1008									1269						
1036									1295						
1064									1284						
1092									1281						

Table 21. Data for Wild15 T. carolina showing straight line distance from release point (in meters) over the course of the study. ActvTime=Active Time, in days.

Wild15

ActvTime	T258	T271	T319	T328	T337	T355	T361	T384	T404	T512	T540	T584
0	0	0	0	0	0	0	0	0	0	0	0	0
1	15	8		2	1		1	3	20	3	10	8
2		10			4		18	22	28			
3	21						18	17	13		21	25
5	52	16							19	3		
7	48			24	6	156	21	18	33		12	73
14					6		28	43	26	31		
21	38	345	458	36	11					37	24	185
28	36	373		43	10	301	20		26		47	355
42	78	246		165	19	301	19	335	21	154	110	342
56	122	246			16	300	18	314	23	144	59	211
70		319			14	302	50	312	21	202	56	298
84	150	161			16	336	59	318	4	1020	97	254
112	156	166			18	501	45		27		41	526
140	214	152			40	1044	49		38		159	346
168		145			125	1021	47				156	347
196		92			299	1023	278				66	337
224		59				996					81	342
252		28				1218					76	
280		51				1240					121	
308		54				1221					126	
336		87				993	669				122	
364		80				699	570				98	
392		42				208	606				376	
420		55				144	854				177	
448		62				100	832				256	
476		24				208	836				170	
504		75				209					197	
532		95				141	783				201	
560		82				209	847				178	
588		66				196	839					
616		78				238	729					
644		70				269	796					
672		66				274	805					282
700		86				287	830					343
728		145				254	867					
756		49				242	753					
784		61				208	736					
812		64					707					
840		61					762					
868		102					704					
896		42					723					
924							713					

Table 22. Maximum straight line distance from release point (MaxDist) and time taken to reach that distance (TimeToMax) for 32 T. carolina monitored at lease one activity year.

Tag Number	MaxDist (m)	TimetoMax (activity days)
261	475	21
271	373	28
284	327	56
316	242	56
520	390	84
323	912	112
535	269	112
584	526	112
425	912	112
355	1044	140
563	883	168
505	354	196
510	365	196
337	299	196
299	226	224
376	125	224
253	118	252
502	878	252
332	641	280
389	358	280
314	176	308
18	313	364
513	124	392
540	376	392
313	113	476
350	643	504
320	131	588
400	366	616
361	867	728
365	1239	924
356	863	1008
343	1295	1036

Table 23. Maximum straight line distance from release point (MaxDist) and time taken to reach that distance (TimeToMax) for 19 T. carolina monitored at lease two activity years.

Tag Number	MaxDist (m)	TimetoMax (activity days)
313	113	476
513	124	392
320	131	588
18	313	364
505	354	196
389	358	280
400	366	616
271	373	28
540	376	392
261	475	21
584	526	112
350	643	504
356	863	1008
361	867	728
502	878	252
323	912	112
355	1044	140
365	1239	924
343	1295	1036

Table 24. Growth in *T. carolina*, grouped by sex and age class. Mean interval (time between inital and last measurement) is only for individuals showing no growth. Data of Nichols (1939) and Stickel and Bunck (1989) are also presented.

FBF Data

Age Class	Sex	n	Mean Initial CL	Mean Annual Growth (mm/yr)	Mean Annual % Growth	Min Annual % Growth	Max Annual % Growth	Standard Deviation	% with no growth	Mean Interval
1	unk	3	83.9	10.2	10.8%	6.1%	16.3%	5.13%	0.0%	na
2	F	19	127.9	2.7	2.1%	0.0%	5.5%	1.71%	10.5%	2 year
2	M	20	135.6	2.3	1.8%	0.3%	6.3%	1.56%	0.0%	na
3	F	15	135.9	0.3	0.3%	0.0%	1.4%	0.39%	40.0%	4.14 year
3	M	39	147.1	0.5	0.4%	0.0%	2.5%	0.51%	28.2%	2.18 year
4	F	5	141.8	0.7	0.4%	0.0%	1.0%	0.38%	20.0%	4 year
4	M	4	145.3	0.0	0.0%	0.0%	0.3%	0.17%	75.0%	3.67 year

Nichols Data

Size Group			Approx	Mean Annual	Mean Annual
MinCL	MaxCL	n	Age Class	Growth (mm/yr)	% Growth
79.6	119.4	6	1	4.6	4.8%
119.4	132.7	6	2	2.0	1.7%
132.7	145.9	12	3 and 4	1.3	1.0%
145.9	159.1	7	3 and 4	1.0	0.7%

Stickel Data

Stickel	Mean Annual % Growth		
Age Group	Male	Female	Cook Age
4-7 yr	5.5%	5.5%	1
8-13 yr	6.7%	5.3%	1 and 2
14-19 yr	2.3%	3.4%	2

Table 25. Analysis of percent average annual growth of carapace in T. carolina by sex and age class.

TWO-WAY				
Source of Variation	df	MS	F	Pr>F
Age	2	29.77	25.68	0.0001
Sex	1	0.30	0.26	0.6133
Age*Sex	2	0.46	0.39	0.6749

Table 26. Results of linear regression analysis of percent average annual growth in T. carolina as a function of initial carapace length (in mm), grouped by sex and age class.

Group	n	r	slope	F	p
age class 1, juvenile	3	0.998	-0.002	273.814	0.038
age class 2, female	19	0.465	-0.001	4.685	0.045
age class 2, male	20	0.654	-0.001	13.438	0.002
age class 3, female	15	0.224	0.000	0.689	0.422
age class 3, male	39	0.207	-0.000	1.659	0.206
age class 4, female	5	0.439	-0.000	0.718	0.459
age class 4, male	4	0.149	0.000	0.046	0.851

Table 27. Survival of radio-tagged T. carolina to 3 and 5 years post-release (by origin, time in holding pen, sex, and age). Percent of all individuals released still alive after 3 and 5 years. **=significant at the p=0.01 level.

SURVIVAL TO 3 YEARS AFTER RELEASE			
	wild (n=27)	pet (n=26)	Chi-square
Origin (wild or pet)	33.3%	34.6%	0.04
	0 days (n=29)	15 days (n=24)	
Holding Pen (0 or 15 days)	34.5%	33.3%	0.04
	Male (n=30)	Female (n=23)	
Sex (M or F)	36.7%	30.4%	0.03
	Age Cat 2 (n=17)	Age Cat 3,4 (n=36)	
Age (class 2 or class 3+4)	5.9%	47.2%	7.05**

SURVIVAL TO 5 YEARS AFTER RELEASE			
	wild (n=15)	pet (n=17)	Chi-square
Origin (wild or pet)	26.6%	23.5%	0.04
	0 days (n=17)	15 days (n=15)	
Holding Pen (0 or 15 days)	23.5%	26.6%	0.04
	Male (n=17)	Female (n=15)	
Sex (M or F)	35.3%	13.3%	1.05
	Age Cat 2 (n=10)	Age Cat 3,4 (n=22)	
Age (class 2 or class 3+4)	0.0%	36.4%	3.10

Table 28. Age-related differences in survival, mortality, and disappearance to 3 and 5 years after release in repatriated T. carolina. *,**=significant at the p=0.05 and 0.01 levels, respectively.

	After 3 yr			After 5 yr		
	age class 2	age class	chi-square (1 df)	age class 2	age class 3+4	chi-square (1 df)
% alive	6%	47%	7.05**	0%	36%	3.10
% dead	47%	39%	0.07	30%	45%	0.19
% unknown	47%	14%	5.18*	70%	18%	6.05*

Table 29. Survival of T. carolina without radios to 3 and 5 years post release (by sex and age category). Percent of individuals still known to be alive after 3 and 5 years.

Survival to 3 years after release

	Male (n=139)	Female (n=143)
By Sex (M or F)	27%	20%

	Age Class 2 (n=116)	Age Class 3+4 (n=166)
By Age (Class 2 or Class 3+4)	26%	21%

By Sex and Age	Male (n=139)	Female (n=143)
Age Class 2 (n=116)	36%	19.70%
Age Class 3+4 (n=166)	22%	19.40%

Logistic Regression Analysis

Model	Akaike Info Criterion	Likelihood Ratio	df	P
# alive after 3 years= age sex	307.062	3.428	2	0.18
# alive after 3 years= age	307.617	0.873	1	0.35
# alive after 3 years= sex	(best model) 305.517	1.973	1	0.16

Survival to 5 years after release

	Male (n=73)	Female (n=79)
By Sex (M or F)	18%	18%

	Age Class 2 (n=73)	Age Class 3+4 (n=79)
By Age (Class 2 or Class 3+4)	19%	16%

By Sex and Age	Male (n=73)	Female (n=79)
Age Class 2 (n=73)	21%	18%
Age Class 3+4 (n=79)	16%	18%

Logistic Regression Analysis

Model	Akaike Info Criterion	Likelihood Ratio	df	P
# alive after 5 years= age sex	148.004	0.202	2	0.90
# alive after 5 years= age	(best model) 146.014	0.192	1	0.66
# alive after 5 years= sex	146.206	0	1	0.99

Table 30. Fecundity rates and annual variation in reproductive effort in female T. carolina repatriated to Floyd Bennett Field (yes=gravid).

Individual	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%
number gravid	1	0	4	7	3	2	
total number	2	1	13	15	4	2	
annual rate	50%	0%	31%	47%	75%	100%	
overall rate							46%

Table 31 Hatching year (HY) and year first recorded (YFR) for young T. carolina on Floyd Bennett Field.

	Year						
Hatch Year	1990	1991	1992	1993	1994	1995	Total 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

Table 32. Total range for all repatriated T. carolina with 10 or more points (calculated by 95% harmonic mean (HM) and 95% bivariate normal (BVN) methods). YR=year released, AGE=age class.

					Period	Covered		Total		Number of points, by year								
ID	CAT	SEX	AGE	YR	From	To	Status	Points	87	88	89	90	91	92	93	94/95	95%HM	95%BVN
T044	92Rad	F	4	89	7/10/89	12/15/93	alive	48			1	1		28	19		22.39	19.92
T074	92Rad	F	2	88	6/27/88	12/17/93	alive	40		14	2	1		10	13		5.45	94.29
T210	92Rad	F	3	88	9/27/88	6/6/94	alive	42		1				31	9	1	44.08	40.25
T293	92Rad	M	4	89	7/10/89	4/18/93	dead	15			1			14			2.92	26.05
T381	92Rad	M	3	88	9/22/88	6/2/94	alive	30		2				23	4	1	12.75	21.64
T489	92Rad	F	4	87	9/1/87	6/19/95	alive	36	1					13	21	2	4.32	24.24
T509	92Rad	M	3	90	7/6/90	8/17/93	mia	17				1		8	8		2.18	11.65
T524	92Rad	F	2	90	7/6/90	12/15/93	alive	51				1		28	22		2.40	4.02
T526	92Rad	F	2	90	7/6/90	8/21/93	mia	48				2		32	14		2.07	4.34
T528	92Rad	F	3	90	6/21/90	10/23/93	mia	51				2		31	19		17.47	28.72
T531	92Rad	M	3	90	10/19/90	10/21/94	alive	51				1		26	21	3	3.13	5.02
T532	92Rad	F	2	90	7/6/90	11/7/92	mia	27				1	1	25			5.46	18.61
T072	93Rad	F	2	88	6/27/88	6/16/94	alive	26		4	2	1		1	16	2	5.65	17.56
T088	93Rad	F	2	87	9/1/87	12/15/93	alive	17	1						16		5.35	50.18
T092	93Rad	F	2	87	8/21/87	6/26/94	alive	21	2	1				1	16	1	15.49	29.70
T310	93Rad	F	3	88	7/27/88	4/20/95	alive	18		1		1			15	1	11.08	21.65
T341	93Rad	F	2	88	7/27/88	6/16/94	alive	23		6	1				13	3	2.91	12.41
T348	93Rad	F	4	88	9/22/88	5/25/95	alive	24		2	1	2			16	3	5.09	18.90
T351	93Rad	F	3	88	8/19/88	6/30/95	alive	21		1					15	5	4.67	16.05
T466	93Rad	F	3	89	7/19/89	9/25/93	mia	16			1		3		12		7.01	4.42
T018	P0	F	2	88	7/11/88	9/24/92	mia	51		30		1		20			2.34	7.38
T020	P0	F	2	88	7/11/88	9/20/88	mia	33		33							5.70	12.70
T075	P0	F	3	88	7/11/88	8/22/88	mia	24		24							0.82	1.58
T089	P0	M	3	88	7/11/88	8/1/88	dead	13		13							0.04	0.19
T320	P0	M	4	88	7/11/88	7/15/91	dead	45		38	7		1				1.05	0.95
T323	P0	M	3	88	7/11/88	7/2/93	mia	92		32	8	13	8	27	8		26.83	17.11
T356	P0	M	3	88	7/11/88	12/17/93	alive	101		34	13	7	5	24	21		13.46	60.23
T457	P0	M	3	89	8/9/89	3/27/90	dead	16			16						5.73	30.77
T505	P0	F	3	90	5/14/90	6/22/95	alive	23				18	4			2	4.45	10.42
T510	P0	M	3	90	5/14/90	3/25/92	dead	27				19	9				3.15	12.56
T513	P0	F	3	90	5/29/90	6/13/94	alive	40				16		12	11	1	1.64	4.26
T563	P0	M	3	90	5/14/90	7/1/91	dead	24				18	6				10.71	27.67

Table 32. Total range for all repatriated T. carolina with 10 or more points (calculated by 95% harmonic mean (HM) and 95% bivariate normal (BVN) methods). YR=year released, AGE=age class.

					Period	Covered		Total		Number of points, by year								
ID	CAT	SEX	AGE	YR	From	To	Status	Points	87	88	89	90	91	92	93	94/95	95%HM	95%BVN
T284	P15	F	2	89	6/7/89	6/19/90	dead	14			13	1					1.38	9.01
T299	P15	M	2	89	6/7/89	7/17/90	dead	26			14	12					1.32	4.53
T313	P15	M	3	88	7/12/88	12/15/93	alive	132		29	20	21	11	34	21		1.81	1.82
T314	P15	F	2	88	7/12/88	5/8/90	dead	11		10		1					0.26	3.24
T332	P15	F	3	88	7/12/88	3/29/90	dead	50		28	23						5.16	51.61
T349	P15	F	3	88	7/12/88	8/30/88	mia	21		21							0.58	15.83
T350	P15	M	3	88	7/12/88	5/1/91	dead	14		13			1				4.49	24.34
T376	P15	M	3	88	8/19/88	6/9/89	dead	19		13	7						0.25	1.32
T389	P15	M	3	88	7/12/88	12/15/93	alive	123		29	18	14	9	34	24		6.27	16.30
T535	P15	F	3	90	6/13/90	9/24/91	mia	23				13	11				1.87	5.34
T253	W0	M	2	89	6/1/89	5/7/91	dead	42			18	21	3				0.97	1.39
T261	W0	M	4	89	6/2/89	12/15/93	alive	64			26	2		17	21		11.72	43.14
T304	W0	F	2	88	7/20/88	9/19/88	mia	20		20							0.05	0.17
T308	W0	M	3	88	7/29/88	10/18/88	dead	22		22							2.94	6.86
T316	W0	F	2	88	7/22/88	3/30/90	dead	40		26	15						1.54	5.29
T324	W0	M	3	88	8/16/88	11/30/88	mia	16		16							0.92	1.17
T334	W0	F	2	88	7/29/88	9/20/88	mia	24		24							14.87	40.34
T343	W0	F	4	88	6/28/88	12/15/93	alive	70		49	6				16		45.22	76.05
T365	W0	F	3	88	6/28/88	6/28/93	dead	44		43					1		29.17	91.83
T370	W0	M	3	88	7/11/88	8/3/89	dead	43		34	9						1.52	2.78
T400	W0	F	3	89	6/20/89	4/3/93	dead	77			17	22	11	29			9.58	16.00
T425	W0	M	2	89	6/27/89	4/23/91	dead	39			20	19	1				18.17	68.77
T502	W0	F	3	90	7/3/90	8/10/92	dead	37				10	11	18			24.87	43.69
T520	W0	M	3	90	7/3/90	9/5/91	dead	19				13	7				16.38	40.28
T258	W15	M	2	89	6/1/89	5/30/90	dead	22			21	1					0.55	3.04
T271	W15	M	3	89	6/17/89	12/15/93	alive	107			21	19	15	34	22		11.74	10.26
T337	W15	F	2	88	8/30/88	3/30/90	dead	37		14	24						4.52	7.40
T355	W15	M	3	88	9/12/88	4/27/95	alive	91		6	34	21	10	23		1	48.03	107.43
T361	W15	M	3	88	8/16/88	6/24/93	mia	93		16	12	10	11	35	12		16.72	72.06
T384	W15	M	2	88	8/16/88	4/17/89	mia	16		16							0.86	11.63
T404	W15	M	3	89	7/5/89	3/30/90	dead	22			22						0.08	0.18
T540	W15	F	3	90	5/27/90	6/22/93	mia	60				15	11	26	9		5.29	11.81
T584	W15	M	3	90	5/27/90	4/20/95	alive	26				16	5		5	1	5.56	17.22

Table 33. Estimated home range and total range size of *T. carolina* that established home ranges after repatriation to Floyd Bennett Field. (HM=harmonic mean, BVN=bivariate normal).

			Total	Number of points by year							HOME RANGE		TOTAL RANGE	
ID	CAT	YR	Points	88	89	90	91	92	93	94/95	95% HM	95% BVN	95% HM	95% BVN
T018	P0	88	21			1		20			1.13	3.20	2.34	7.38
T044	92Rad	89	46					28	19		8.25	11.96	22.39	19.92
T072	93Rad	88	20			1		1	16	2	1.97	3.74	5.65	17.56
T074	92Rad	88	23					10	13		4.89	29.12	5.45	94.29
T088	93Rad	87	16						16		3.18	39.82	5.35	50.18
T092	93Rad	87	19	1				1	16	1	6.73	19.05	15.49	29.70
T210	92Rad	88	41					31	9	1	42.57	33.32	44.08	40.25
T253	W0	89	24			21	3				0.51	1.60	0.97	1.39
T261	W0	89	37					17	21		4.04	7.64	11.72	43.14
T271	W15	89	87			19	15	34	22		6.12	6.94	11.74	10.26
T293	92Rad	89	14					14			0.52	2.04	2.92	26.05
T310	93Rad	88	17			1			15	1	4.44	10.65	11.08	21.65
T313	P15	88	103		20	21	11	34	21		1.68	1.67	1.81	1.82
T316	W0	88	15		15						0.39	3.48	1.54	5.29
T323	P0	88	53			13	8	27	8		7.16	6.94	26.83	17.11
T332	P15	88	23		23						0.92	2.80	5.16	51.61
T341	93Rad	88	16						13	3	0.71	1.92	2.91	12.41
T343	W0	88	16						16		1.38	4.73	45.22	76.05
T348	93Rad	88	21			2			16	3	7.23	13.78	5.09	18.90
T351	93Rad	88	20						15	5	3.03	14.81	4.67	16.05
T355	W15	88	33				10	23		1	5.59	14.77	48.03	107.43
T356	P0	88	55				5	24	21		11.30	16.33	13.46	60.23
T361	W15	88	47					35	12		1.22	2.35	16.72	72.06
T381	92Rad	88	28					23	4	1	5.16	15.70	12.75	21.64
T389	P15	88	95		18	14	9	34	24		4.27	5.03	6.27	16.30
T400	W0	89	61			22	11	29			9.91	16.92	9.58	16.00
T425	W0	89	20			19	1				4.04	14.97	18.17	68.77
T466	93Rad	89	15				3		12		1.93	2.23	7.01	4.42
T489	92Rad	87	35					13	21	2	2.85	15.13	4.32	24.24
T502	W0	90	28				11	18			5.76	7.12	24.87	43.69
T509	92Rad	90	16					8	8		0.24	0.57	2.18	11.65
T513	P0	90	24					12	11	1	0.87	3.65	1.64	4.26
T524	92Rad	90	49					28	22		2.56	4.01	2.40	4.02
T526	92Rad	90	45					32	14		0.86	1.82	2.07	4.34
T528	92Rad	90	49					31	19		15.00	10.64	17.47	28.72
T531	92Rad	90	50					26	21	3	2.83	3.80	3.13	5.02
T532	92Rad	90	26				1	25			4.97	18.93	5.46	18.61
T535	P15	90	11				11				0.24	1.67	1.87	5.34
T540	W15	90	46				11	26	9		5.88	11.31	5.29	11.81
T584	W15	90	11				5		5	1	0.33	4.58	5.56	17.22

Table 34. Multi-variate analysis of variance of home range stability in repatriated *T. carolina*. Significance indicates inter-year shift in center of home range. *,**,***,=significant at p=0.05, 0.01, 0.001, and level respectively.

ID	SEX	89vs90	90vs91	90vs92	91vs92	92vs93
T044	F					p=0.000***
T400	F		ns		p=0.000***	
T489	F					p=0.000***
T502	F				p=0.002**	
T524	F					ns
T526	F					p=0.003**
T528	F					p=0.018*
T540	F				p=0.001**	
T261	M					ns
T271	M		p=0.001***		ns	p=0.009**
T313	M	p=0.045*	ns		ns	p=0.007**
T323	M			p=0.000***		
T355	M				p=0.000****	
T356	M					ns
T361	M					ns
T389	M	ns		ns		ns
T531	M					p=0.000***

Table 35. Distance (m) between consecutive year's hibernacula in repatriated *T. carolina*, by individuals and time period. For example, for Tag44, the hibernaculum used during winter 1992-93 was 106.2 m from hibernaculum used in 1991-92.

Tag	H88-89	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

Table 36. Use of habitat by repatriated *T. carolina* on Floyd Bennett Field. Number of active season points in each of seven available habitat types.

Tag	Sex	Lawn	DecFor	Shrub	GrassHerb	Phrag	shore	Wetland	Total
T018	F	0	0	14	5	2	0	0	21
T044	F	0	3	26	15	0	0	0	44
T072	F	0	0	15	5	0	0	0	20
T074	F	0	1	17	5	0	0	0	23
T088	F	0	6	9	1	0	0	0	16
T092	F	0	0	11	6	0	0	0	17
T210	F	0	0	25	14	1	0	0	40
T253	M	0	13	0	1	9	0	0	23
T261	M	0	0	14	7	15	0	0	36
T271	M	0	35	17	6	26	0	0	84
T293	M	0	0	10	3	0	0	0	13
T310	F	0	7	9	0	1	0	0	17
T313	M	0	69	5	0	27	0	0	101
T316	F	0	1	0	0	10	0	0	11
T323	M	0	40	9	4	0	0	0	53
T332	F	0	9	0	0	13	0	0	22
T341	F	1	11	0	0	4	0	0	16
T343	F	0	3	10	2	1	0	0	16
T348	F	0	3	9	7	0	0	0	19
T351	F	0	0	8	2	10	0	0	20
T355	M	0	0	22	4	6	0	0	32
T356	M	0	23	22	4	0	0	0	49
T361	M	0	0	44	2	0	0	0	46
T381	M	0	4	4	0	19	0	0	27
T389	M	0	0	75	6	6	0	0	87
T400	F	0	17	9	3	28	0	0	57
T425	M	0	13	4	2	1	0	0	20
T466	F	0	7	5	2	0	0	0	14
T489	F	0	1	14	12	6	0	1	34
T502	F	0	1	19	8	0	0	0	28
T509	M	0	2	14	0	0	0	0	16
T513	F	0	3	3	2	16	0	0	24
T524	F	0	17	2	4	26	0	0	49
T526	F	0	0	29	14	0	0	0	43
T528	F	0	1	36	11	0	0	0	48
T531	M	0	2	31	11	6	0	0	50
T532	F	0	8	11	3	4	0	0	26
T535	F	0	1	6	3	1	0	0	11
T540	F	0	2	9	4	31	0	0	46
T584	M	0	0	7	2	2	0	0	11
Total		1	303	574	180	271	0	1	1330

Table 37. Absolute and proportionate amounts of habitat types within the availablity polygon on Floyd Bennett Field.

45 A. Pavement included.

Habitat	Area (ha)	Percent
Paved	21.76	13.73%
Lawn	1.34	0.85%
DecFor	18.51	11.68%
Shrub	45.70	28.84%
GrassHer	36.73	23.18%
Phrag	32.95	20.79%
Bayshore	0.72	0.45%
Wetland	0.74	0.47%
Total	158.44	100.00%

45 B. Pavement excluded.

Habitat	Area (ha)	Percent
Lawn	1.34	0.98%
DecFor	18.51	13.54%
Shrub	45.70	33.44%
GrassHer	36.73	26.87%
Phrag	32.95	24.11%
Bayshore	0.72	0.53%
Wetland	0.74	0.54%
Total	136.68	100.00%

45 C. Pavement excluded, woody types combined.

Habitat	Area (ha)	Percent
Lawn	1.34	0.98%
Woody	64.21	46.98%
GrassHer	36.73	26.87%
Phrag	32.95	24.11%
Bayshore	0.72	0.53%
Wetland	0.74	0.54%
Total	136.68	100.00%

Table 38. Habitat selection by T. carolina repatriated to Floyd Bennett Field, based on seven habitat types. *=significant deviation from random habitat use at the p=0.05 level, A=avoidance, P=preference, N=neutral. Avoidance and preference were only determined for individuals showing non-random use of habitat.

Tag Number	Sex	chi-square	df	Lawn	DecFor	Shrub	Grass	Phrag	Shore	Wet-land
T018	F	12.14	6							
T044	F	22.49*	6	A	N	P	N	A	A	A
T072	F	18.30*	6	A	A	P	N	A	A	A
T074	F	18.95*	6	A	N	P	N	A	A	A
T088	F	15.99*	6	A	N	N	A	A	A	A
T092	F	12.17	6							
T210	F	25.07*	6	A	A	P	N	A	A	A
T253	M	46.03*	6	A	P	A	A	N	A	A
T261	M	11.28	6							
T271	M	68.96*	6	A	P	A	A	N	A	A
T293	M	12.58	6							
T310	F	18.78*	6	A	N	N	A	A	A	A
T313	M	277.77*	6	A	P	A	A	N	A	A
T316	F	27.39*	6	A	N	A	A	P	A	A
T323	M	175.62*	6	A	P	A	A	A	A	A
T332	F	37.06*	6	A	N	A	A	P	A	A
T341	F	50.37*	6	N	P	A	A	N	A	A
T343	F	8.04	6							
T348	F	6.85	6							
T351	F	11.06	6							
T355	M	19.76*	6	A	A	P	N	N	A	A
T356	M	61.48*	6	A	P	N	A	A	A	A
T361	M	80.20*	6	A	A	P	A	A	A	A
T381	M	34.62*	6	A	N	A	A	P	A	A
T389	M	109.63*	6	A	A	P	A	A	A	A
T400	F	42.34*	6	A	N	A	A	P	A	A
T425	M	45.74*	6	A	P	N	N	A	A	A
T466	F	18.25*	6	A	P	N	N	A	A	A
T489	F	9.05	6							
T502	F	19.33*	6	A	A	P	N	A	A	A
T509	M	22.48*	6	A	N	P	A	A	A	A
T513	F	24.76*	6	A	N	A	A	P	A	A
T524	F	53.25*	6	A	P	A	A	P	A	A
T526	F	32.46*	6	A	A	P	N	A	A	A
T528	F	42.29*	6	A	A	P	N	A	A	A
T531	M	20.07*	6	A	A	P	N	N	A	A
T532	F	9.94	6							
T535	F	2.88	6							
T540	F	47.87*	6	A	A	N	A	P	A	A
T584	M	5.18	6							
Summed chi-square		1578.43	240							
Pooled chi-square		694.75*	6	A	P	P	A	A	A	A
Heterogeneity chi-square		973.68*	234							
Index of Preference/Avoidance				-1.00	-0.03	0.03	-0.62	-0.31	-1.00	-1.00
Among Inds		1231.00	195							
individuals random	11									
individuals not random	29		avoid	28	10	11	18	16	29	29
			prefer	0	9	12	0	7	0	0
			neutral	1	10	6	11	6	0	0

Table 39. Habitat selection by *T. carolina* repatriated to Floyd Bennett Field, all woody habitats combined. *=significant deviation from random habitat use at the p=0.05 level. A=avoidance, P=preference, N=neutral. Avoidance and preference were only determined for individuals showing non-random use of habitat.

Tag Number	Sex	chi-square	df	Lawn	Woody	Grass	Phrag	Shore	Wet-land
T018	F	4.09	5						
T044	F	15.72	5	A	P	N	A	A	A
T072	F	8.60	5						
T074	F	11.03	5						
T088	F	14.17	5	A	P	A	A	A	A
T092	F	6.03	5						
T210	F	11.60	5	A	N	N	A	A	A
T253	M	7.41	5						
T261	M	6.58	5						
T271	M	19.50	5	A	P	A	N	A	A
T293	M	5.95	5						
T310	F	15.30	5	A	P	A	A	A	A
T313	M	44.35	5	A	P	A	N	A	A
T316	F	26.91	5	A	A	A	P	A	A
T323	M	44.56	5	A	P	A	A	A	A
T332	F	17.71	5	A	N	A	P	A	A
T341	F	10.62	5						
T343	F	7.67	5						
T348	F	6.73	5						
T351	F	8.30	5						
T355	M	6.72	5						
T356	M	40.19	5	A	P	A	A	A	A
T361	M	43.91	5	A	P	A	A	A	A
T381	M	33.51	5	A	N	A	P	A	A
T389	M	53.88	5	A	P	A	A	A	A
T400	F	25.89	5	A	N	A	P	A	A
T425	M	11.71	5	A	P	N	A	A	A
T466	F	8.96	5						
T489	F	5.68	5						
T502	F	10.92	5						
T509	M	18.06	5	A	P	A	A	A	A
T513	F	24.06	5	A	N	A	P	A	A
T524	F	25.13	5	A	N	A	P	A	A
T526	F	15.60	5	A	P	N	A	A	A
T528	F	22.09	5	A	P	N	A	A	A
T531	M	8.36	5						
T532	F	7.40	5						
T535	F	1.90	5						
T540	F	47.56	5	A	A	A	P	A	A
T584	M	1.34	5						
Summed chi-square		705.7	200						
Pooled chi-square		596.3	5	A	P	A	A	A	A
Heterogeneity chi-square		109.3	195						
Index of Preference/Avoidance				-1	0.523	-0.76	-0.24	-1	-1
Among Inds		676.9	156						
individuals random	19								
individuals not random	21		avoid	21	2	16	12	21	21
			prefer	0	13	0	7	0	0
			neutral	0	6	5	2	0	0

Table 40. Patterns of habitat selection by repatriated male and female T. carolina. Based on individuals that established home ranges on Floyd Bennett Field. ***=significant deviation from habitat use at the p=0.001 level. A=avoid, P=prefer, N=neutral.

ID	Sex	chi-square	df		Lawn	Woody	Grass	Phrag	Shore	Wet
Between Sexes		45.78***	4							
Summed chi-square	F	359.70***	125							
Pooled chi-square	F	224.09***	5		A	P	A	A	A	A
Heterogeneity chi-square		135.61	120							
Index of Preference/Avoidance					-1.00	0.25	-0.67	0.00	-1.00	-1.00
Among Females		382.33***	96							
	Individuals		13							
	Individuals		12	Avoid	12	2	8	6	12	12
				Prefer	0	5	0	6	0	0
				Neutral	0	5	4	0	0	0
Summed chi-square	F-Gravid	150.04***	60							
Pooled chi-square	F-Gravid	273.96***	5		N	P	A	A	A	A
Heterogeneity chi-square		123.92***	55							
Summed chi-square	F-not gravid	209.61***	65							
Pooled chi-square	F-not gravid	134.91***	5		A	P	A	P	A	N
Heterogeneity chi-square		74.70	60							
Gravid vs Not Gravid		206.63***	4							
Summed chi-square	M	346.04***	75							
Pooled chi-square	M	426.74***	5		A	P	A	A	A	A
Heterogeneity chi-square		80.70	70							
Index of Preference/Avoidance					-1.00	0.89	-0.89	-0.56	-1.00	-1.00
Among Males		175.63***	56							
	Individuals		6							
	Individuals		9	Avoid	9	0	8	6	9	9
				Prefer	0	8	0	1	0	0
				Neutral	0	1	1	2	0	0

Table 41. Analysis of seasonal habitat use by repatriated T. carolina at Floyd Bennett Field (A=avaoidance, P=preference, N=neutral).

Group	Between Season	Season	Within Season	Lawn	Woody	Grass	Phrag	Shore	Wet
All Inds	p=0.453	1	p<0.001	A	P	A	A	A	A
		2	p<0.001	A	P	A	N	A	A
		3	p<0.001	A	P	A	N	A	A
		4	p<0.001	A	P	A	N	A	A
Males	p=0.199	1	p<0.001	A	P	A	A	A	A
		2	p<0.001	A	P	A	N	A	A
		3	p<0.001	A	P	A	N	A	A
		4	p<0.001	A	P	A	N	A	A
Females	p=0.156	1	ns	A	A	N	N	A	A
		2	ns	n	N	N	N	A	A
		3	p<0.05	A	N	A	N	A	A
		4	p<0.001	A	P	A	N	A	A
Gravid	p=0.105	1	p<0.025	A	P	N	A	A	A
		2	ns	n	N	N	A	A	A
		3	p<0.005	A	P	N	A	A	A
		4	p<0.001	A	P	A	A	A	A
Non-Gravid	p=0.407	1	ns	A	N	A	N	A	A
		2	ns	A	N	N	N	A	A
		3	p<0.001	A	N	A	P	A	A
		4	ns	A	N	A	N	A	A

Table 42. Analysis of monthly habitat use by repatriated *T. carolina* at Floyd Bennett Field (A=avoidance, P=preference, N=neutral).

GROUP	Between Month	Month	Within Month	Lawn	Woody	Grass	Phrag	Shore	Wet
All Inds	p=0.132	April/May	p<0.001	A	P	A	A	A	A
		June	p<0.001	A	P	A	N	A	A
		July	p<0.001	A	P	A	N	A	A
		August	p<0.001	A	P	A	N	A	A
		September	p<0.001	A	P	A	N	A	A
		Oct/Nov	p<0.001	A	P	A	N	A	A
Males	p=0.447	April/May	p<0.001	A	P	A	A	A	A
		June	p<0.001	A	P	A	N	A	A
		July	p<0.001	A	P	A	N	A	N
		August	p<0.001	A	P	A	N	A	A
		September	p<0.001	A	P	A	N	A	A
		Oct/Nov	p<0.001	A	P	A	N	A	A
Females	p=0.178	April/May	p<0.01	A	P	A	N	A	A
		June	ns	N	N	N	N	N	A
		July	ns	A	N	N	N	A	N
		August	ns	A	N	N	N	A	A
		September	ns	A	N	N	N	A	A
		Oct/Nov	p<0.001	A	P	A	N	A	A
Gravid	p=0.082	April/May	p<0.01	A	P	N	A	A	A
		June	ns	A	P	N	N	A	A
		July	p<0.025	A	P	N	A	A	N
		August	ns	A	P	N	N	A	A
		September	p<0.050	A	P	N	A	A	A
		Oct/Nov	p<0.001	A	P	A	A	A	A
Non-Gravid	p=0.448	April/May	p<0.025	A	N	A	N	A	A
		June	ns	A	N	N	N	A	A
		July	ns	A	N	N	N	A	N
		August	ns	A	N	A	N	A	A
		September	p<0.005	A	N	N	P	A	A
		Oct/Nov	ns	A	N	N	N	A	A

Table 43. Habitats used for hibernation by radio-telemetered T. carolina repatriated to Floyd Bennett Field. W=woody, G=grassland, P=Phragmites.

Tag	H88-89	H89-90	H90-91	H91-92	H92-93	H93-94	H94-95	# W	#G	#P
18	W							1		
44				W	W	W		3		
72						W		1		
74						W		1		
88					W	W		2		
210				W	W			2		
253		W	W					2		
261		W			W	P		2		1
271		P	P	P	W	P		1		4
293					W died			1		
310		W				W	W	3		
313	P	P	P	P	P	P				6
314	W							1		
316	P	P died								2
320	W							1		
323	W		W	W	W			4		
324	P									1
326	P died									1
332	P	W died						1		1
337	P	G died							1	1
341						W		1		
343	W					W		2		
348						W		1		
351						P	W	1		1
355	W	W	W	W				4		
356	W		W		W	W		4		
361	W		W	W	W			4		
370	W							1		
376	G								1	
381						W		1		
384	W							1		
389	W	W	W	W	W	W		6		
400		W	W	P	P died			2		2
404		W died						1		
425		W	W died					2		
457		W died						1		
489					W	W		2		
502			W	W				2		
505			W					1		
510			P	W died				1		1
513			P			P				2
520			W					1		
524					P	P				2
526				W	W			2		
528				W	W	W		3		
531				W		W		2		
532					W			1		
535			W					1		
540			P	P	P					3
563			W					1		
584			W			W	W	3		
Total								78	2	28

Table 44. A comparison of mean annual percent growth between *C. picta* repatriated to RAG versus populations in southeastern Pennsylvania (Ernst 1971) and Long Island, NY (Zweifel 1989). n=sample size.

Males

PL	RAG (n)	PA (Ernst1971)	LI (Zweifel 1989)
40-49			38.1%(43)
50-59			
60-69			18.7%(45)
70-79		3.7%(2)	
80-89	6.5%(4)	3.3%(6)	7.0%(79)
90-99	3.3%(9)	1.2%(19)	3.1%(39)
100-109	1.4%(17)	1.1%(12)	3.4%(12)
110-119	1.2%(9)	0.9%(18)	2.4%(7)
120-129	0.0%(5)		0.0%(1)
130-139	0.8%(5)		

Females

PL	RAG	PA (Ernst1971)	LI (Zweifel 1989)
50-59			39.1%(20)
60-69	18.8%(1)		
70-79			18.2%(20)
80-89	16.4%(4)	6.9%(2)	11.4%(17)
90-99	8.1%(6)	2.6%(3)	9.6%(15)
100-109	4.6%(8)	2.2%(7)	9.2%(11)
110-119	3.5%(9)	1.7%(18)	3.4%(15)
120-129	1.0%(3)	0.5%(13)	1.0%(49)
130-139	1.4%(19)	1.1%(8)	
140-149	0.6%(16)		
150-159	1.3%(1)		
160-169	0.3%(8)		

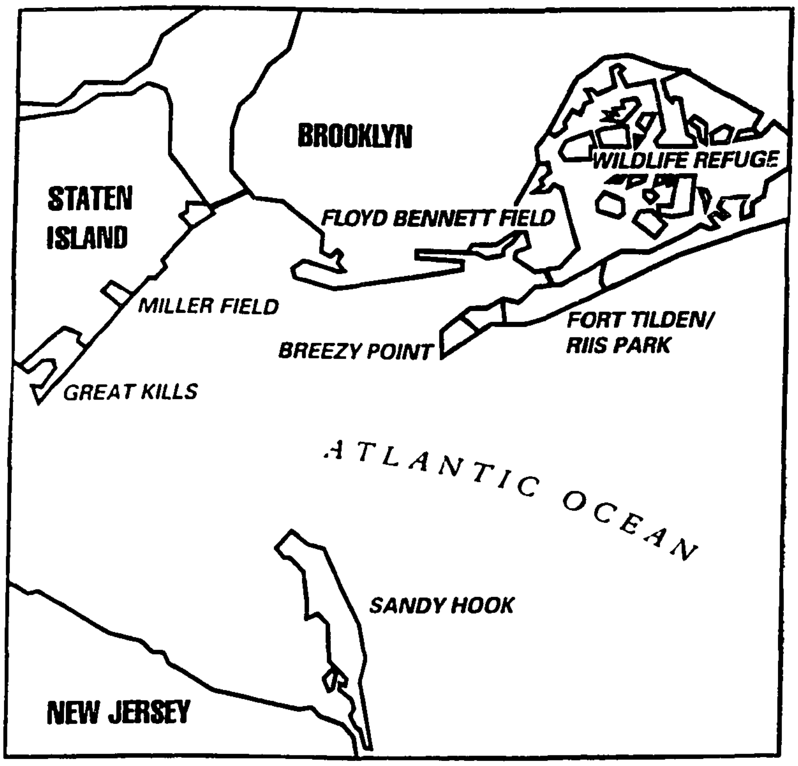

Figure 1. General vicinity of Floyd Bennett Field.

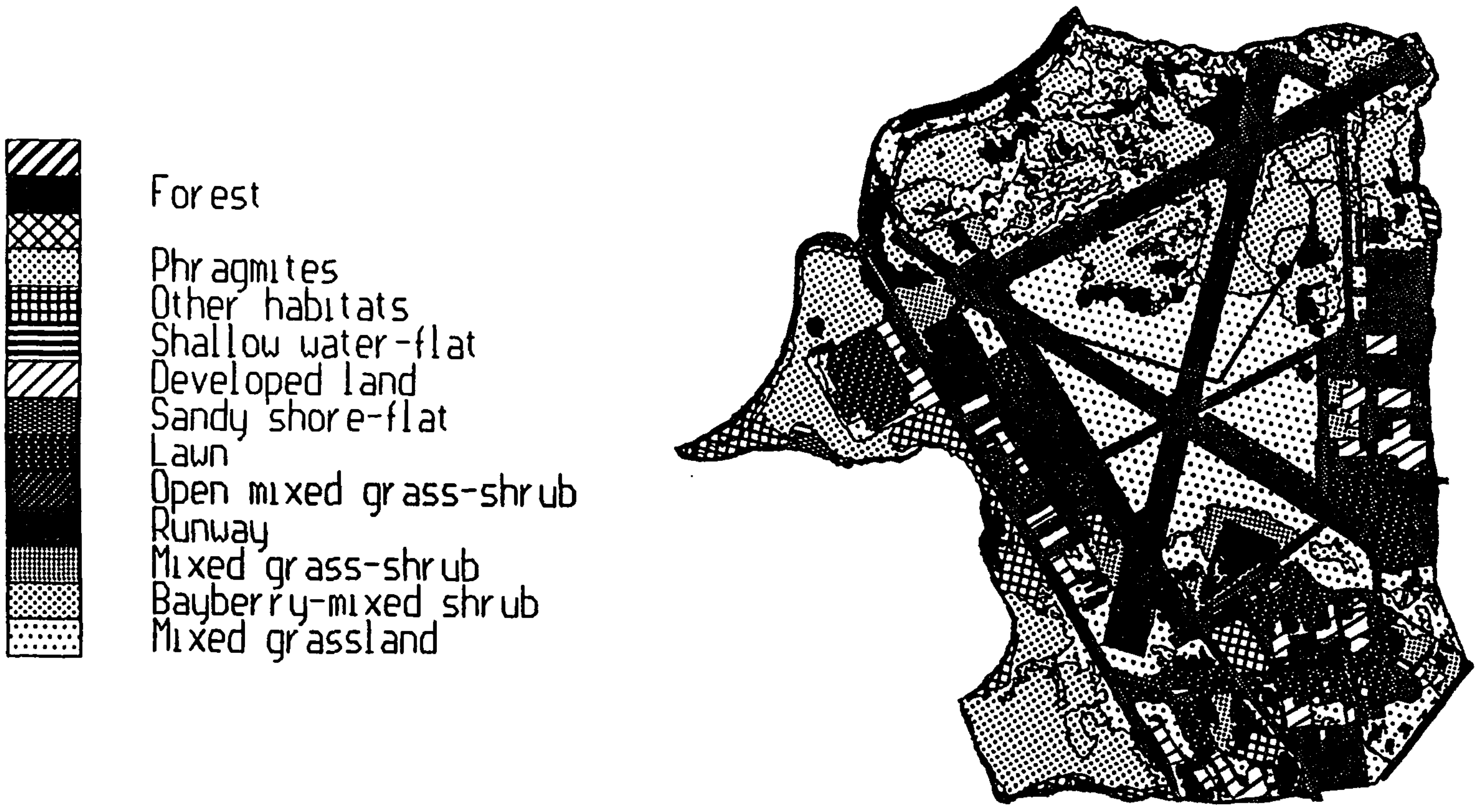

Figure 2. Vegetation of Floyd Bennett Field in 1992. Heavy line defines availability polygon used in habitat analysis

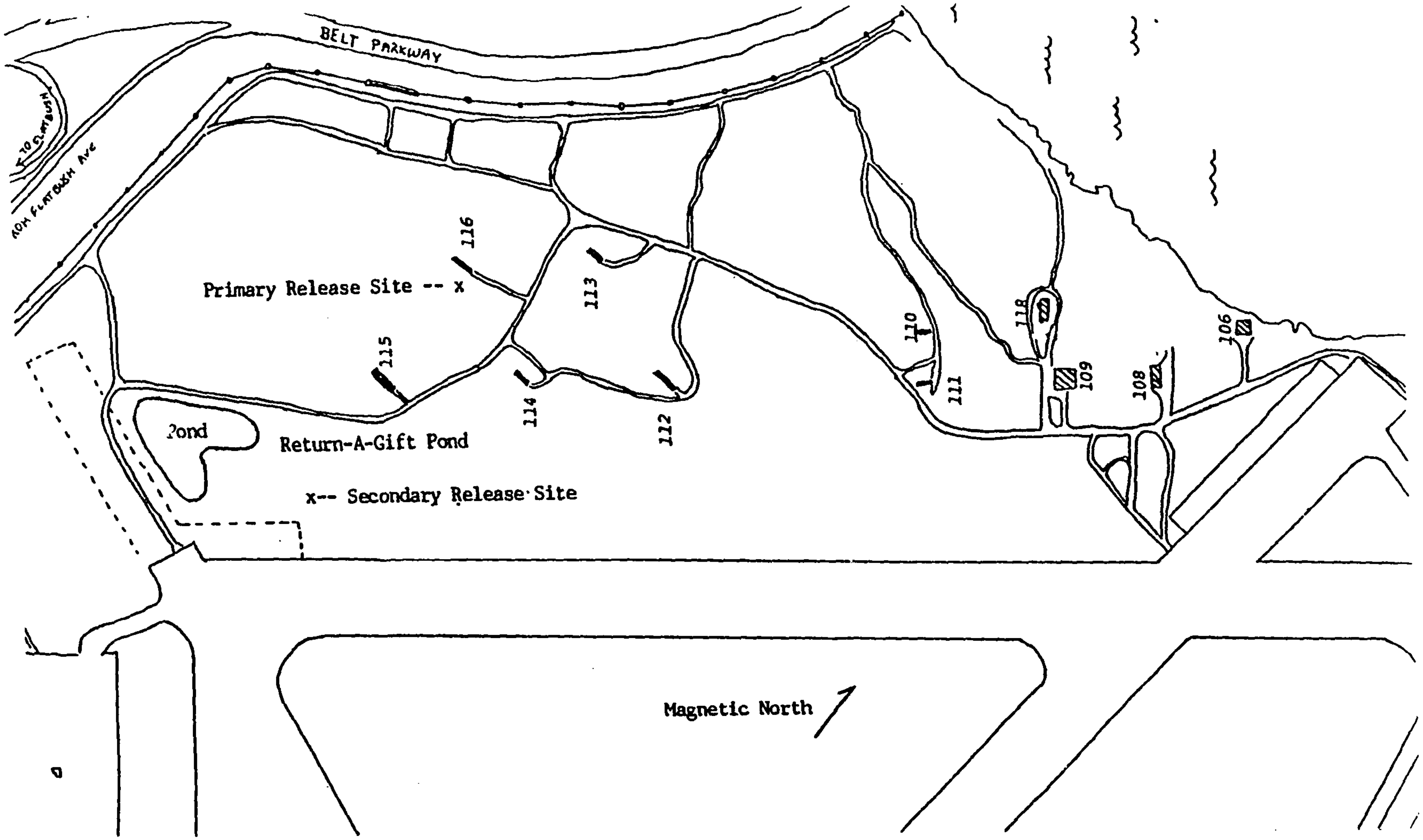

Figure 3. Section of Floyd Bennet Field showing where C. picta were released, and T. carolina release sites. Scale=1:8,000

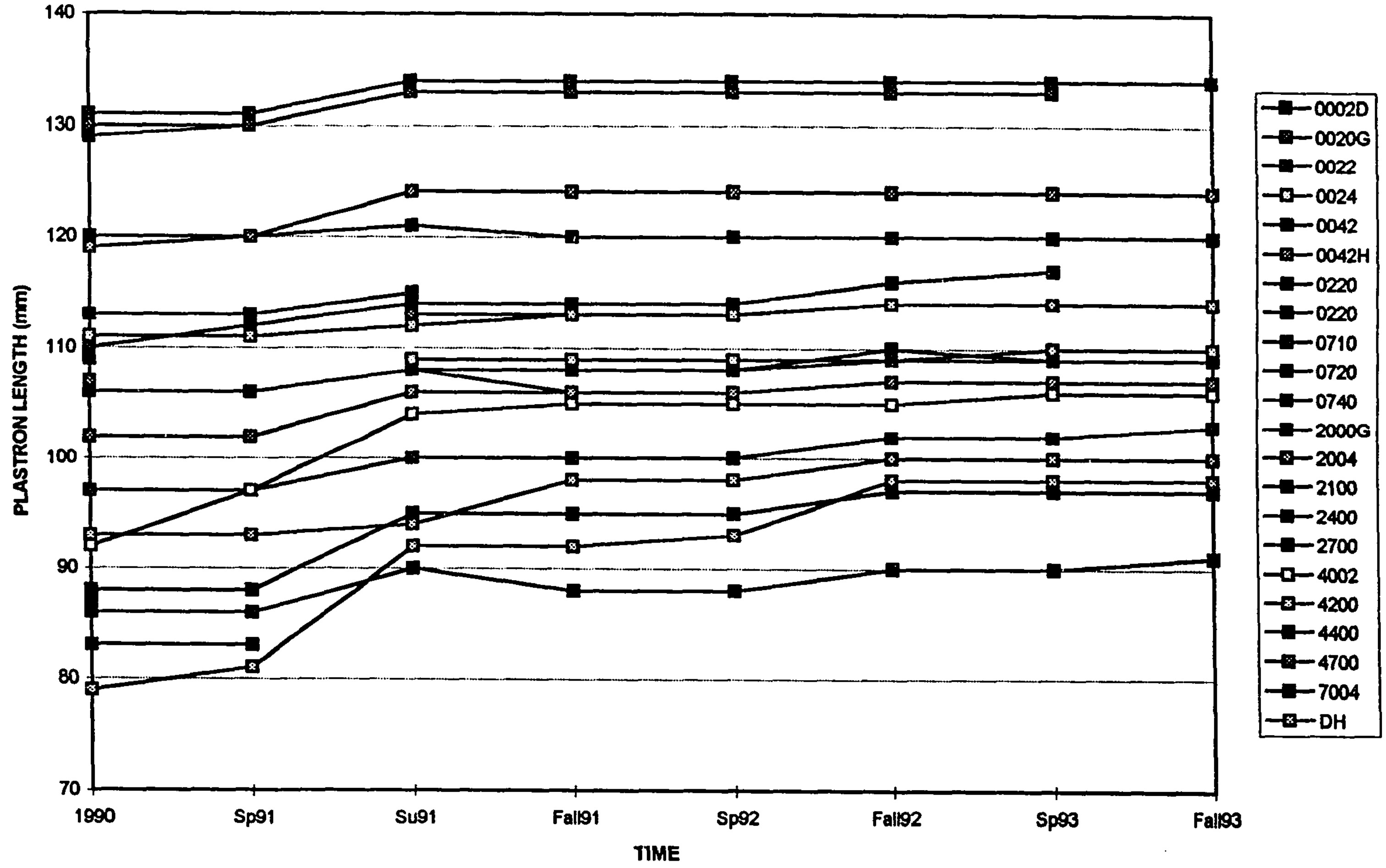

Figure 4. Plastron growth in adult male (PL> 80 mm) C. picta repatriated to Return-A-Gift pond, Floyd Bennett Field in 1990.

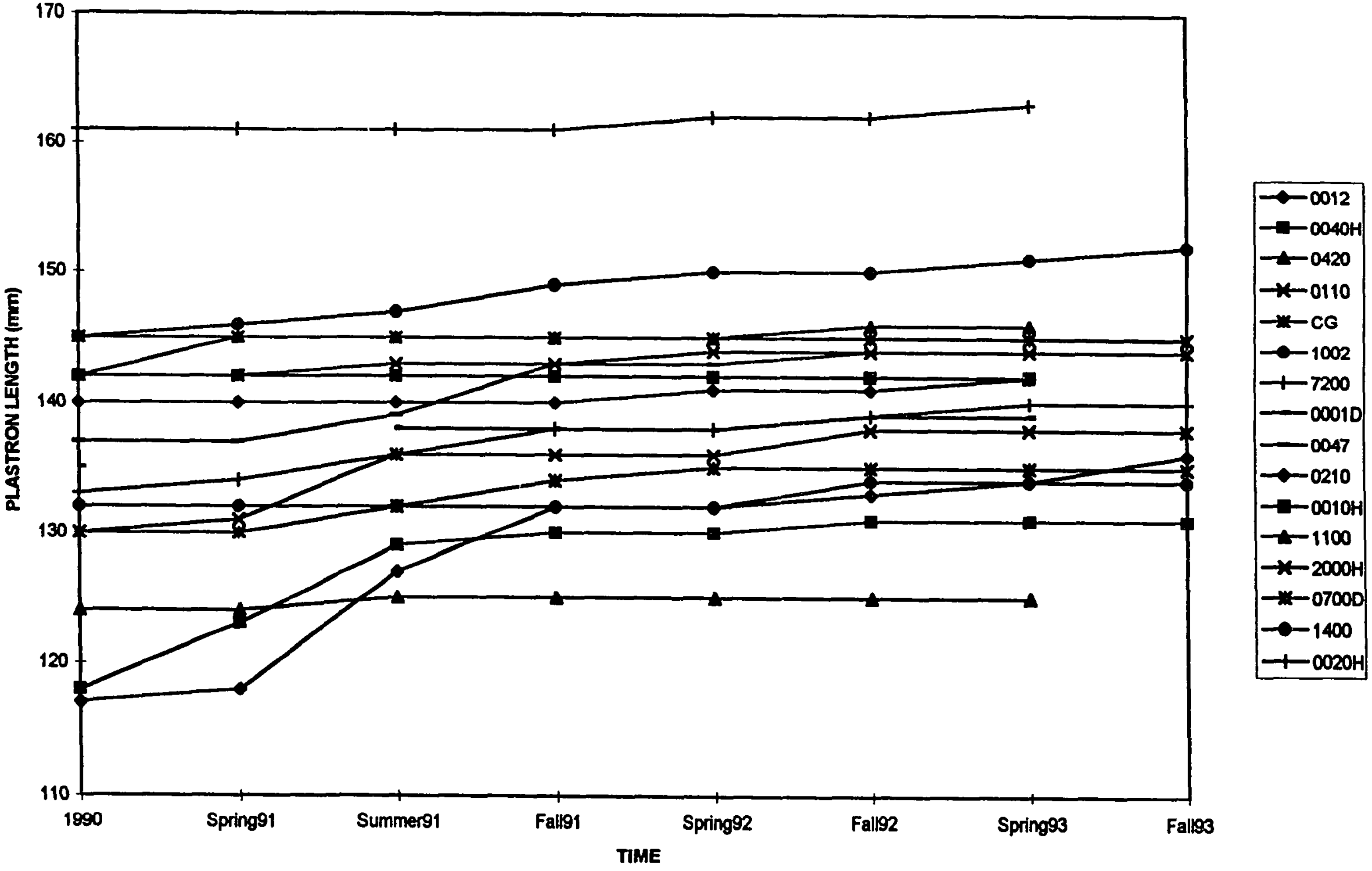

Figure 5. Plastron growth in adult female C. picta (PL>110 mm) repatriated to Return-A-Gift pond, Floyd Bennett Field in 1990.

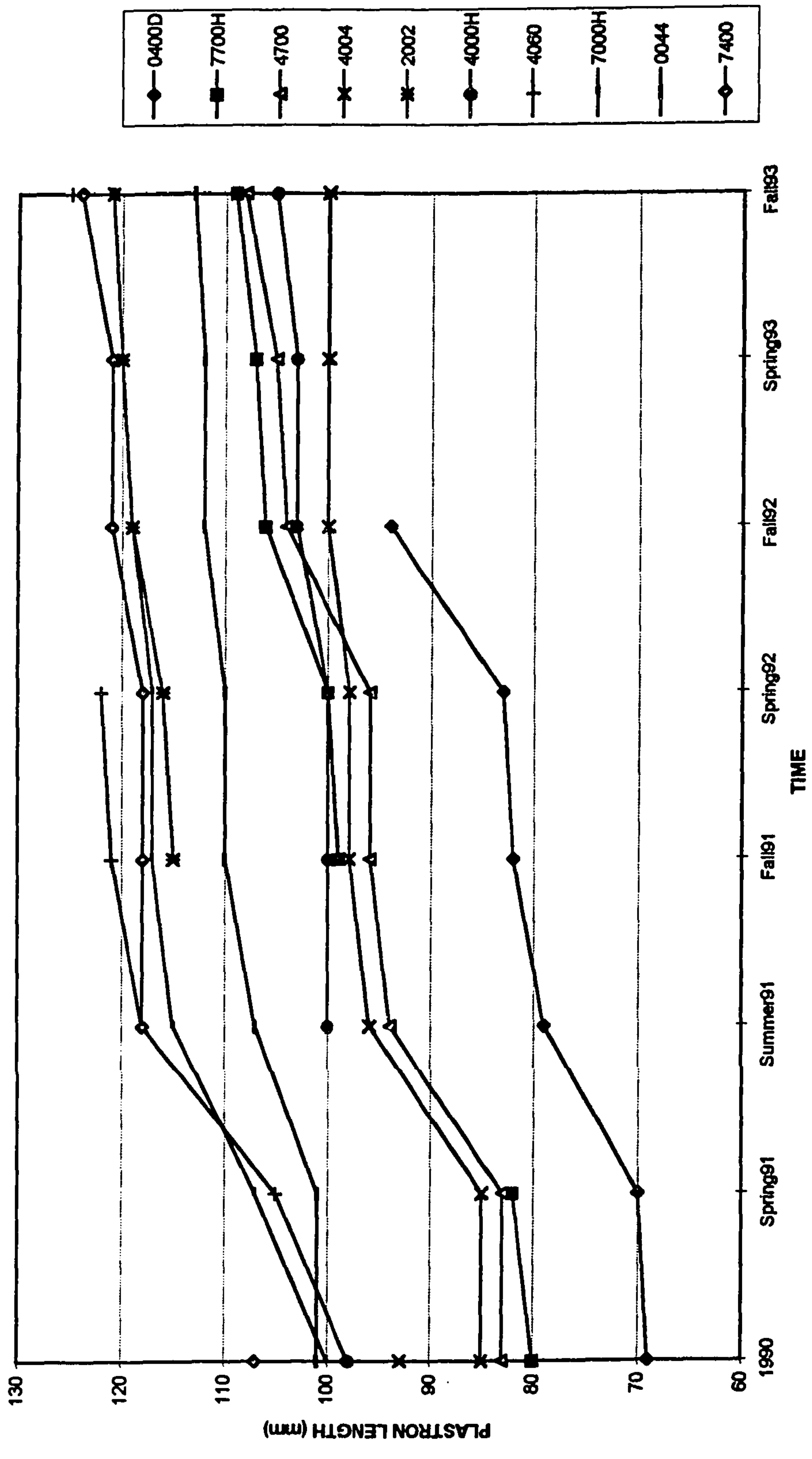

Figure 6. Plastron growth in immature female C. picta (PL<110mm), repatriated to Return-A-Gift pond, Floyd Bennett Field in 1990.

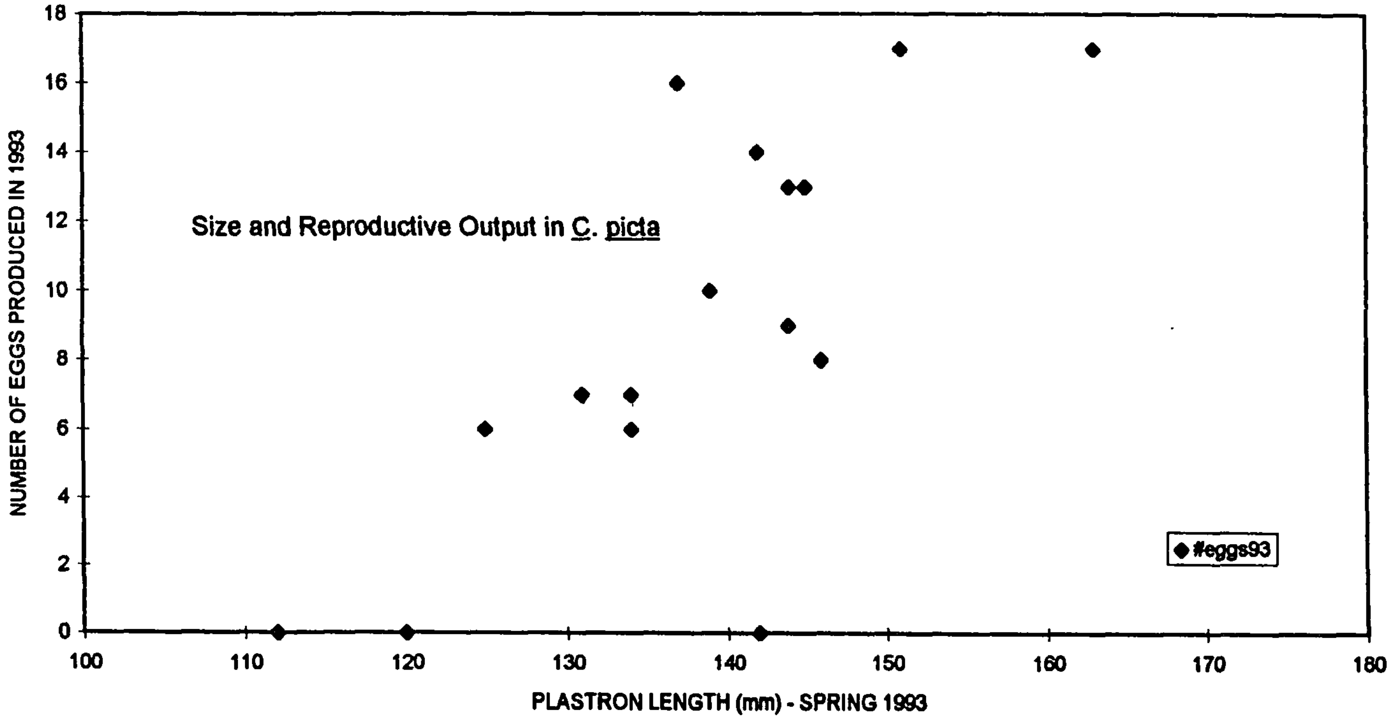

Figure 7. Relationship between annual reproductive output and plastron length (Spearman correlation coeffecient=0.62, p=0.014).

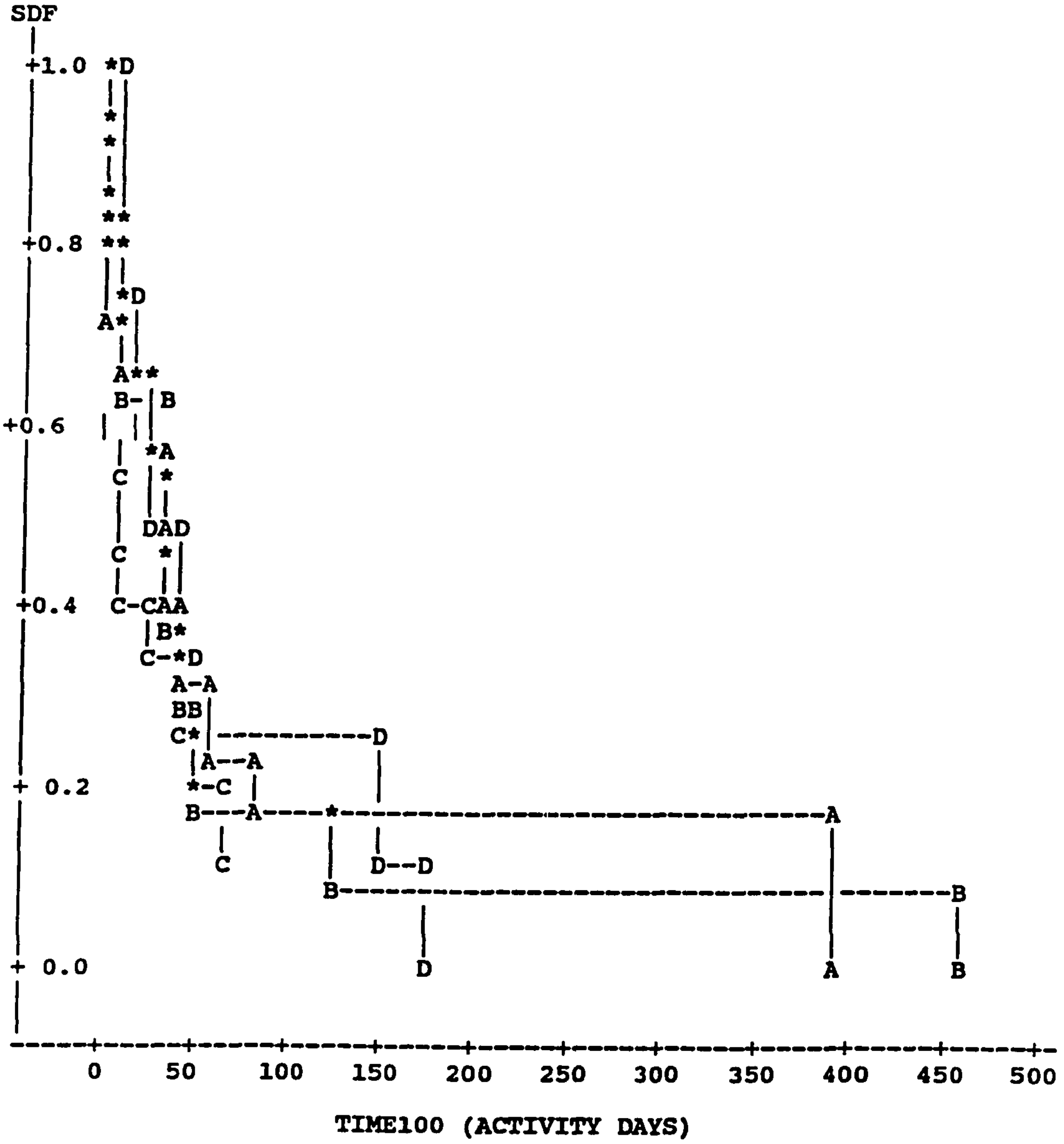

Figure 8. Survival distribution function (SDF) of time100 in T. carolina repatriated to Floyd Bennett Field (A=pet0, B=pet15, C=wild0, D=wild15, *=multiple values).

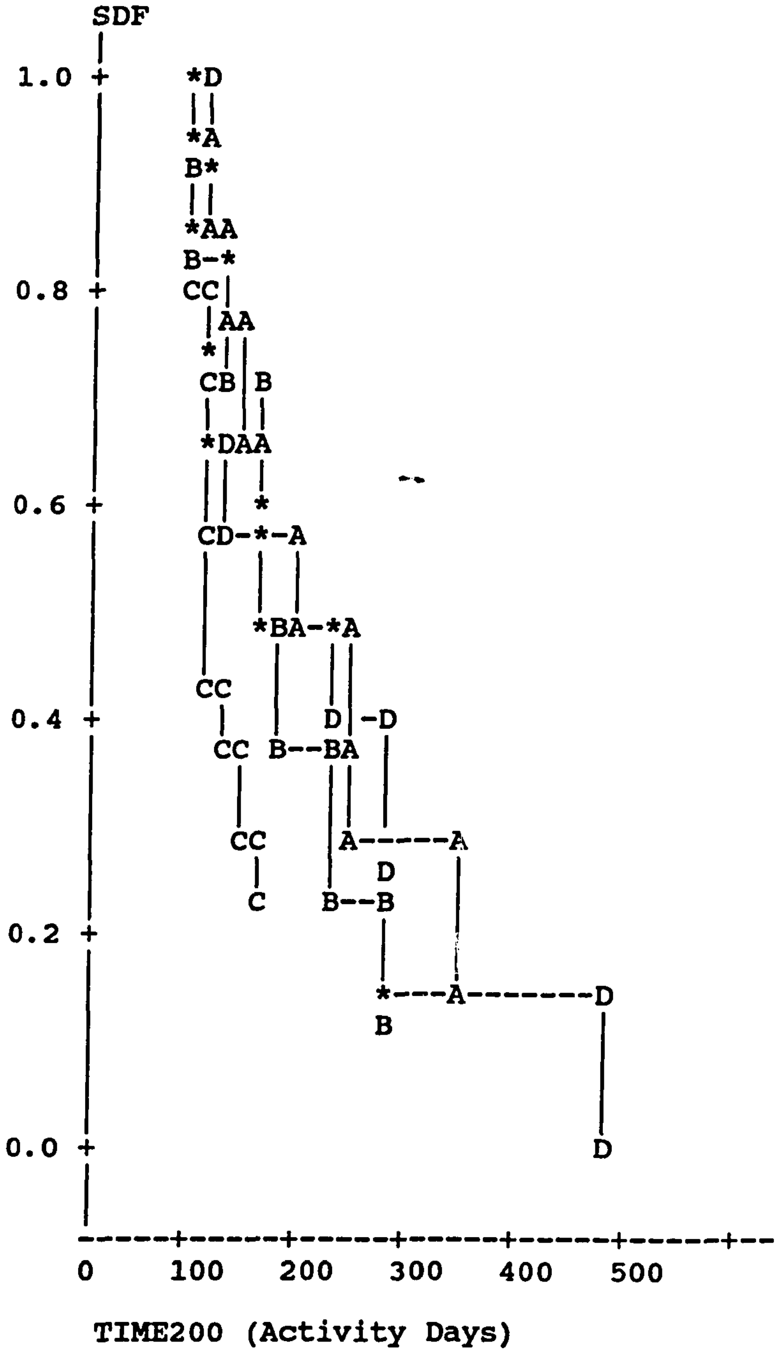

Figure 9. Survival distribution function (SDF) of time_200 in T. carolina repatriated to Floyd Bennett Field (A=pet0, B=pet15, C=wild0, D=wild15, *=multiple values).

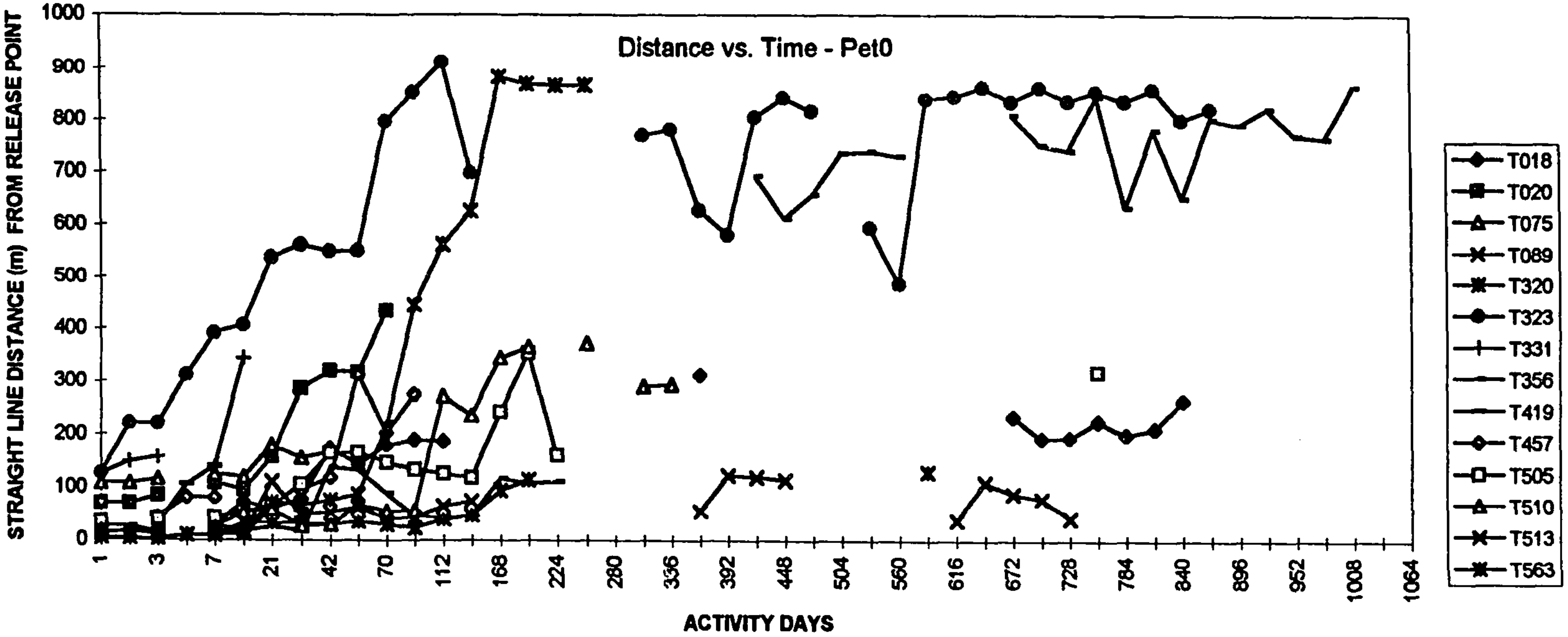

Figure 10. Straight line distance from release point over time, for Pet0 T. carolina repatriated to Floyd Bennett Field.

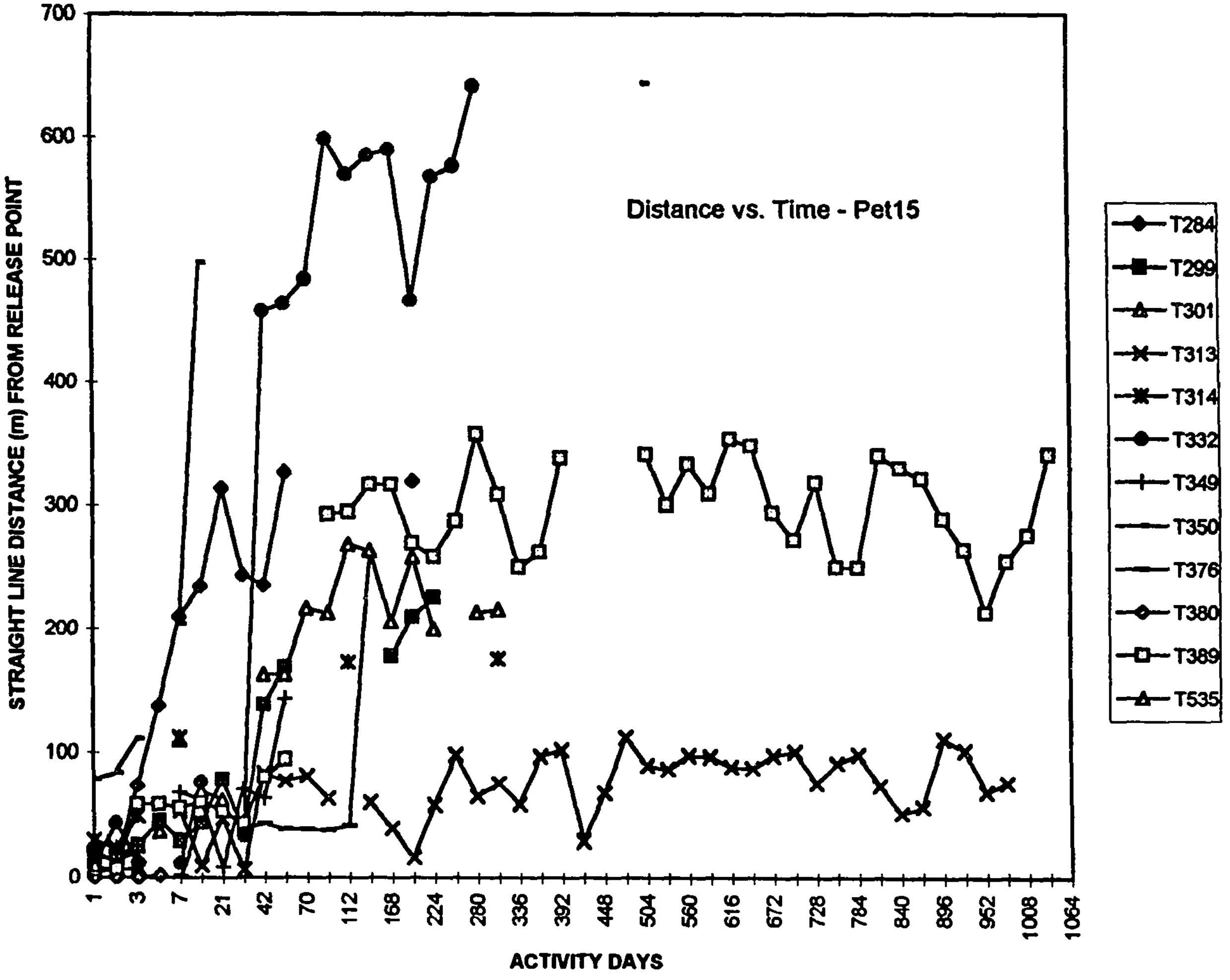

Figure 11. Straight line distance from release point over time, for pet15 T. carolina repatriated to Floyd Bennett Field.

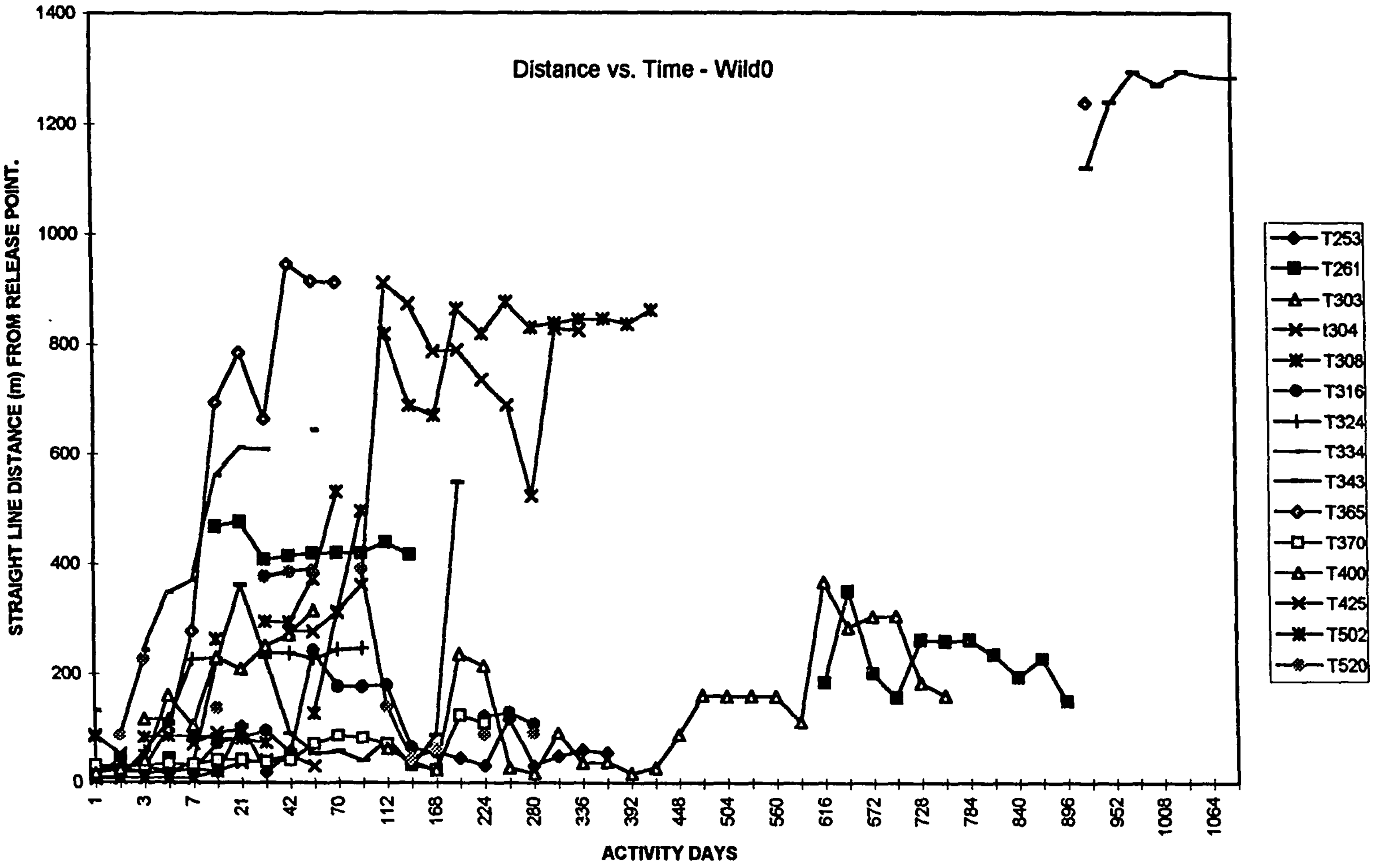

Figure 12. Straight line distance from release point, over time, for wild0 *T. carolina* repatriated to Floyd Bennett Field.

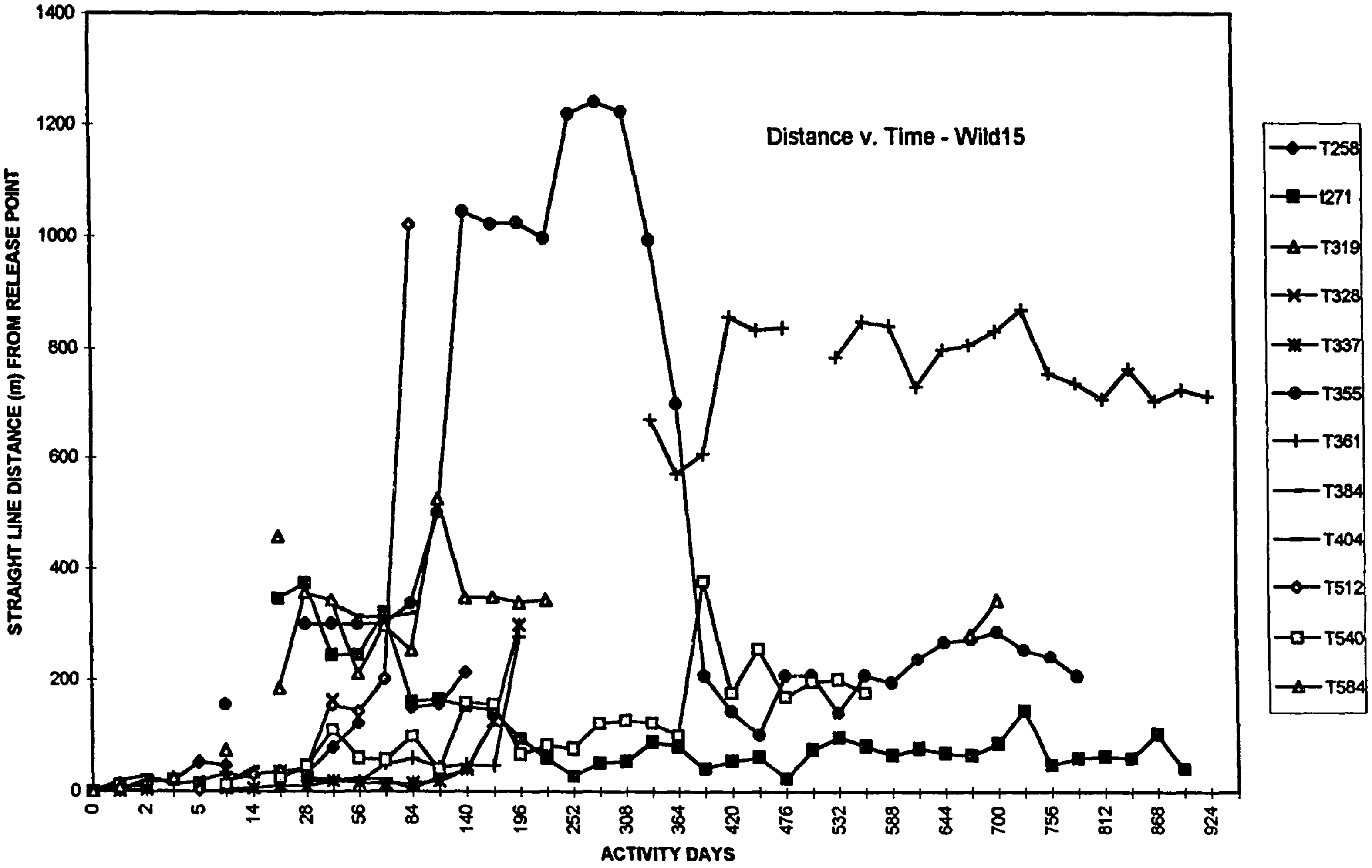

Figure 13. Straight line distance from release point, over time, for wild15 T. carolina repatriated to Floyd Bennett Field.

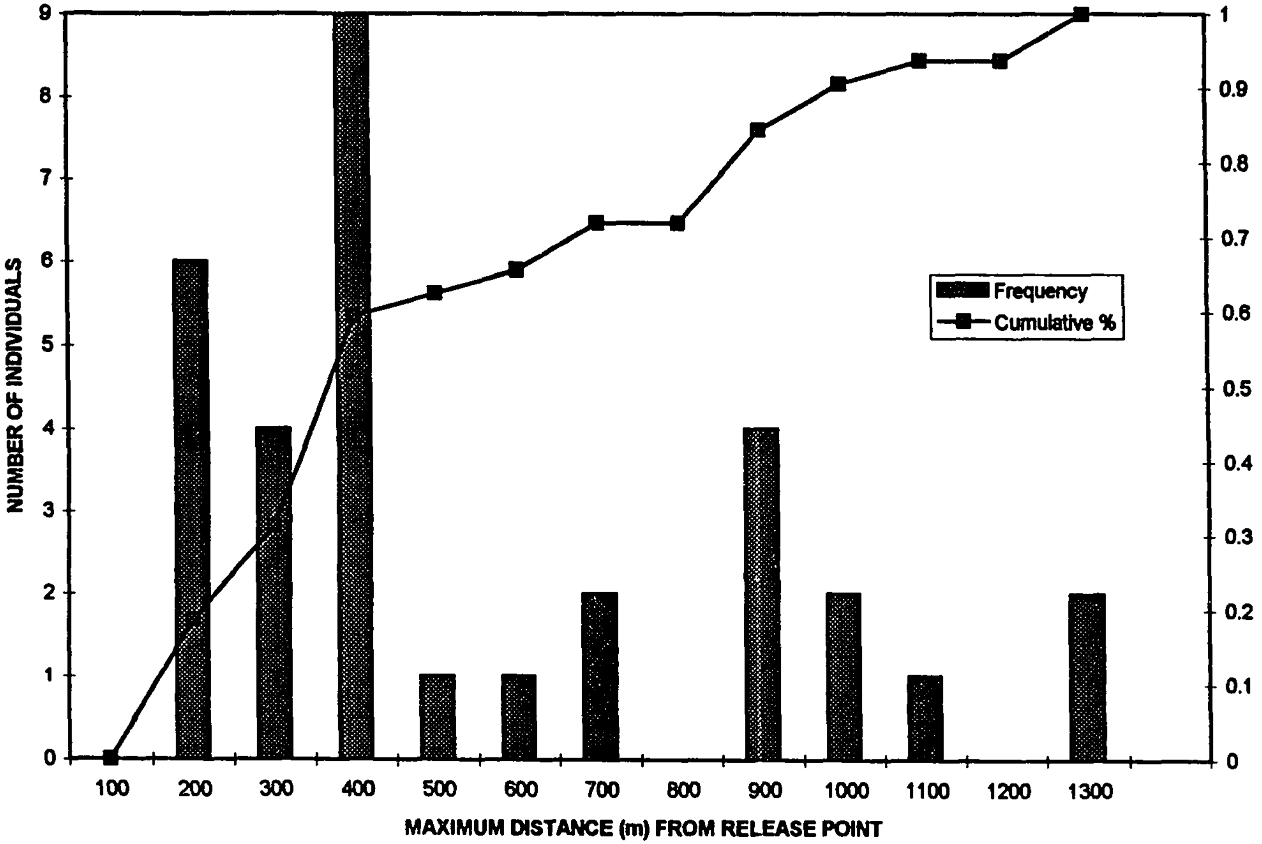

Figure 14. Frequency distribution of maximum distance from release point. Based on 32 T. carolina monitored a minimum of one activity year.

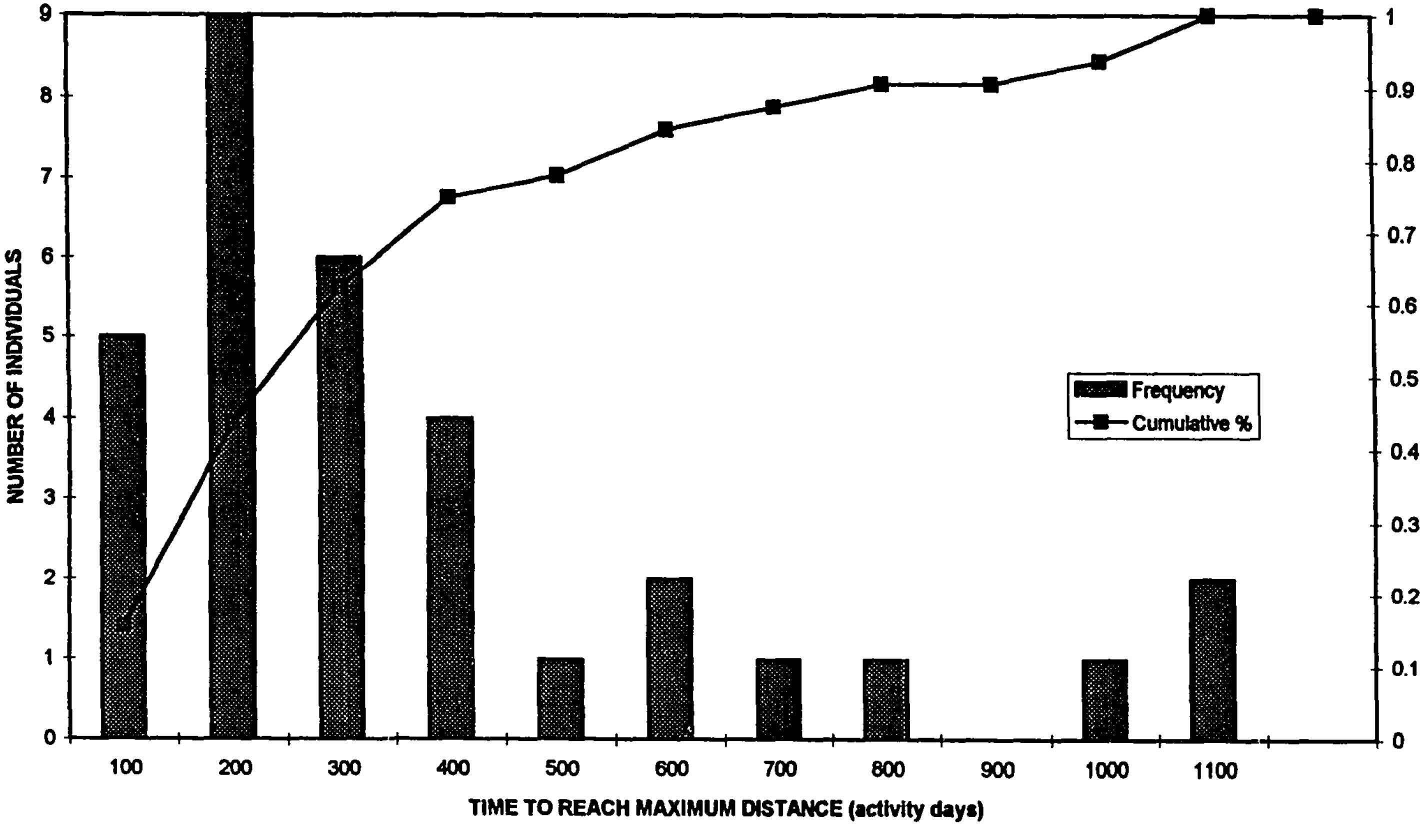

Figure 15. Frequency distribution of time taken by T. carolina to attain maximum distance from release point. Based on 32 individuals monitored at least one activity season .

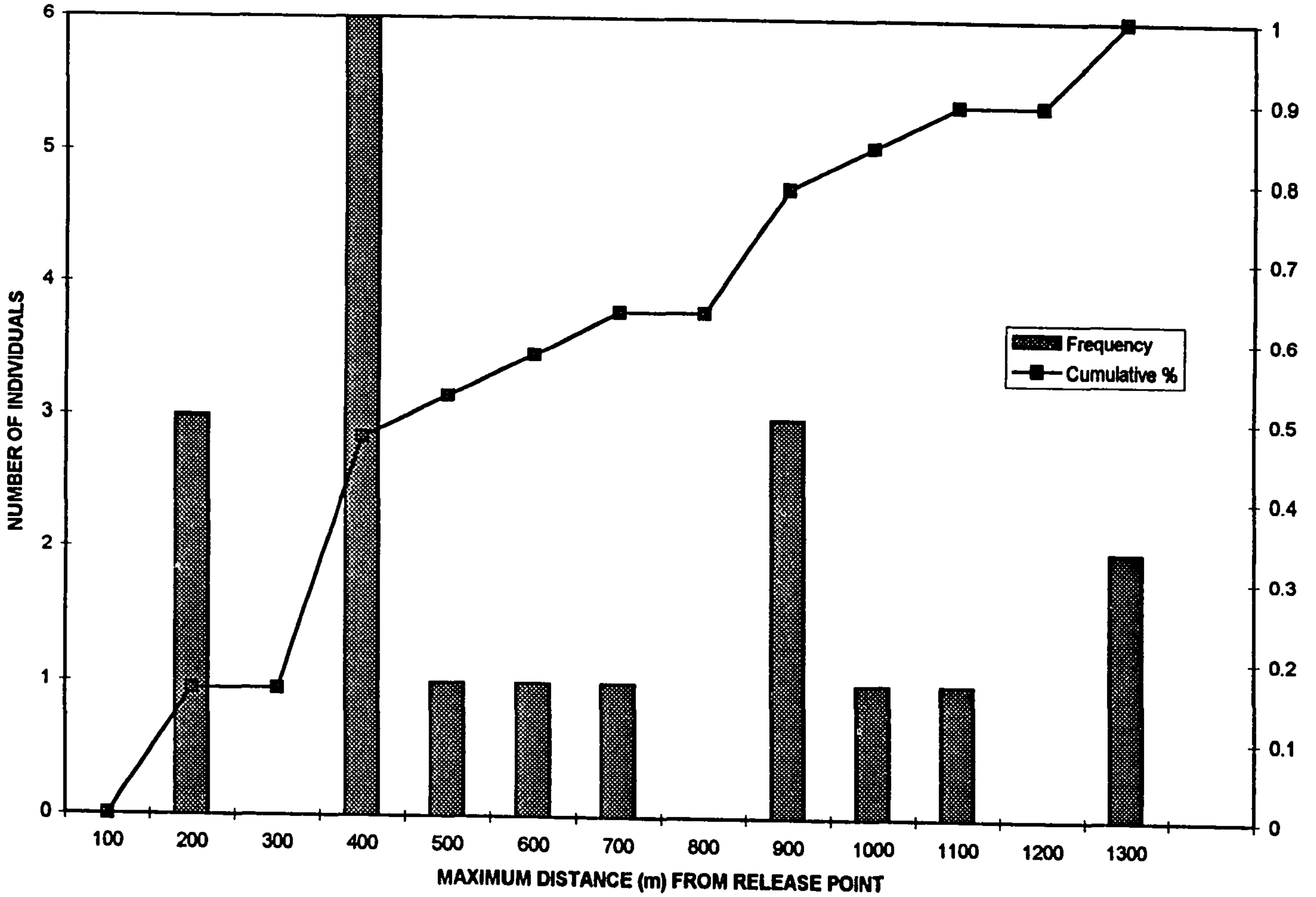

Figure 16. Frequency distribution of maximum distance from release point in T. carolina. Based on 19 individuals monitored at least two activity years.

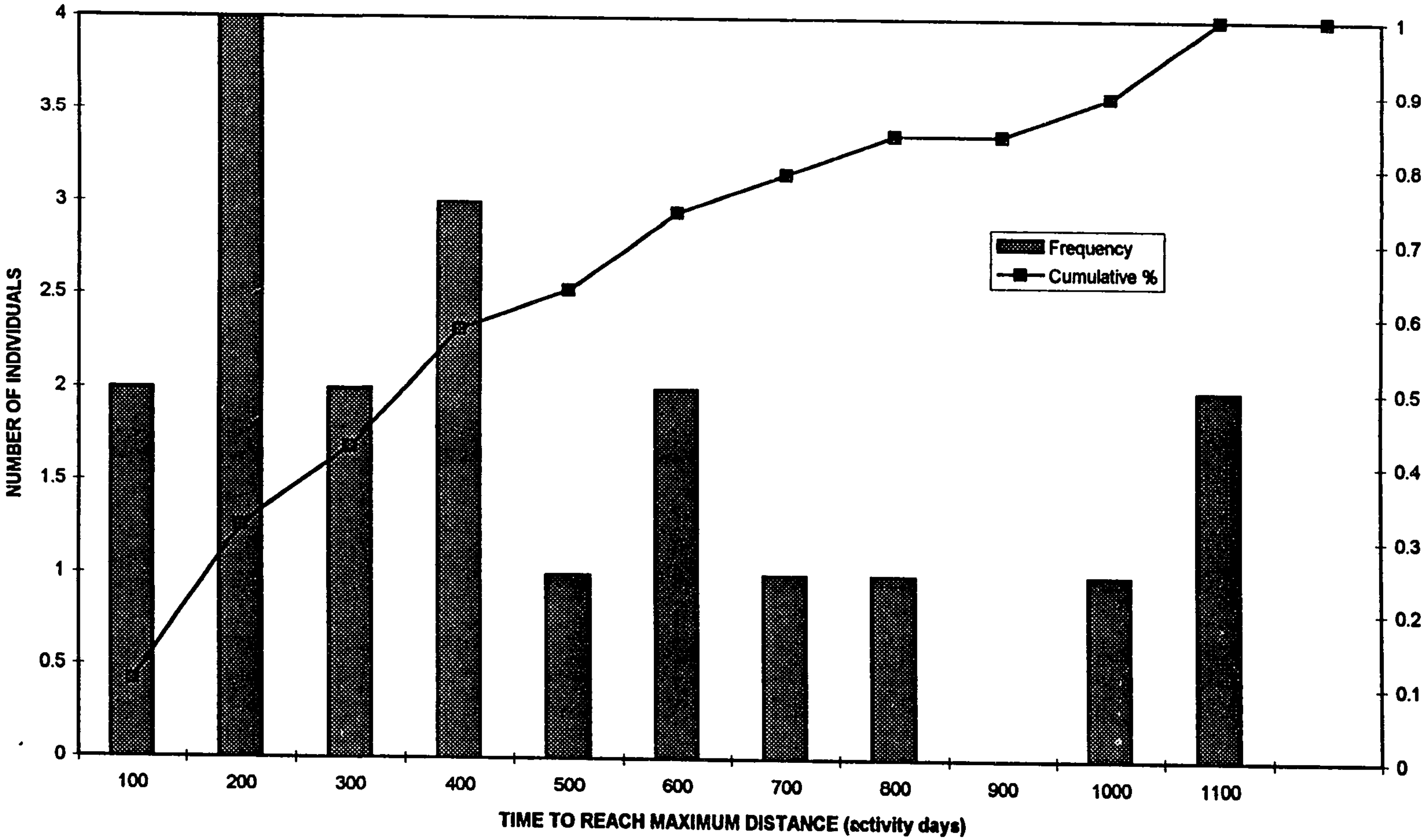

Figure 17. Frequency distribution of time taken by T. carolina to attain maximum distance from release point. Based on 19 individuals monitored at least two activity years.

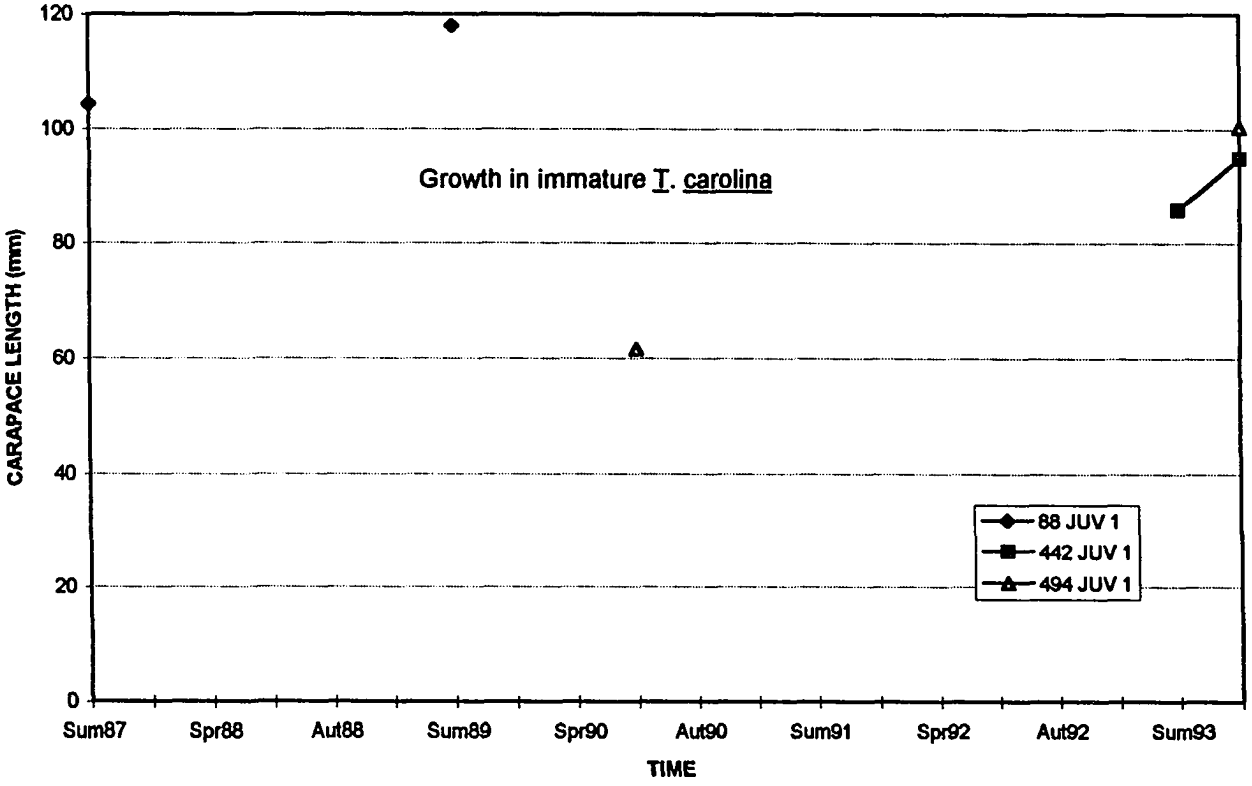

Figure 18. Carapace length growth (mm) in immature (age class 1) T. carolina repatriated to Floyd Bennett Field.

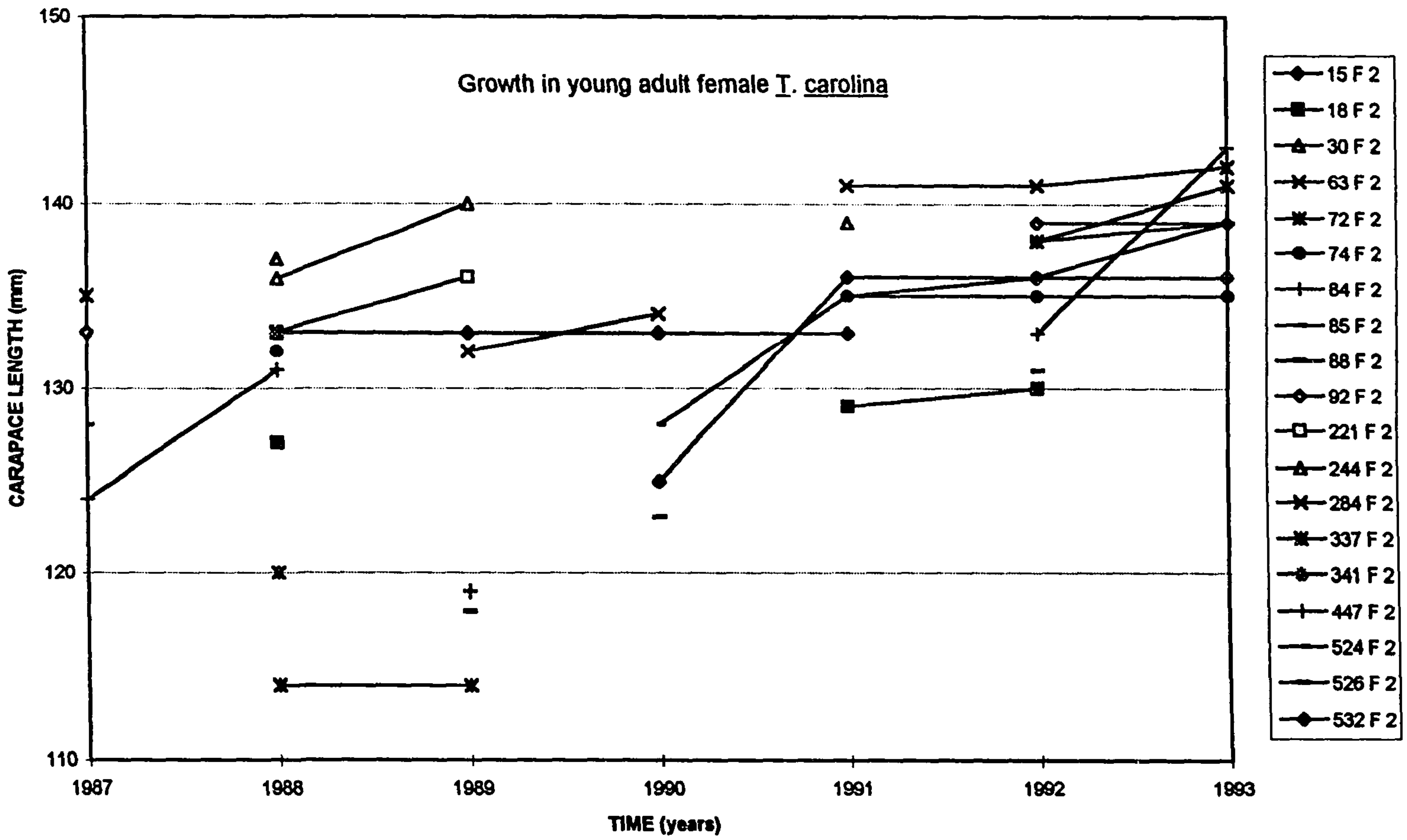

Figure 19. Carapace length growth (mm) in young adult (age class 2) female T. carolina repatriated to Floyd Bennett Field.

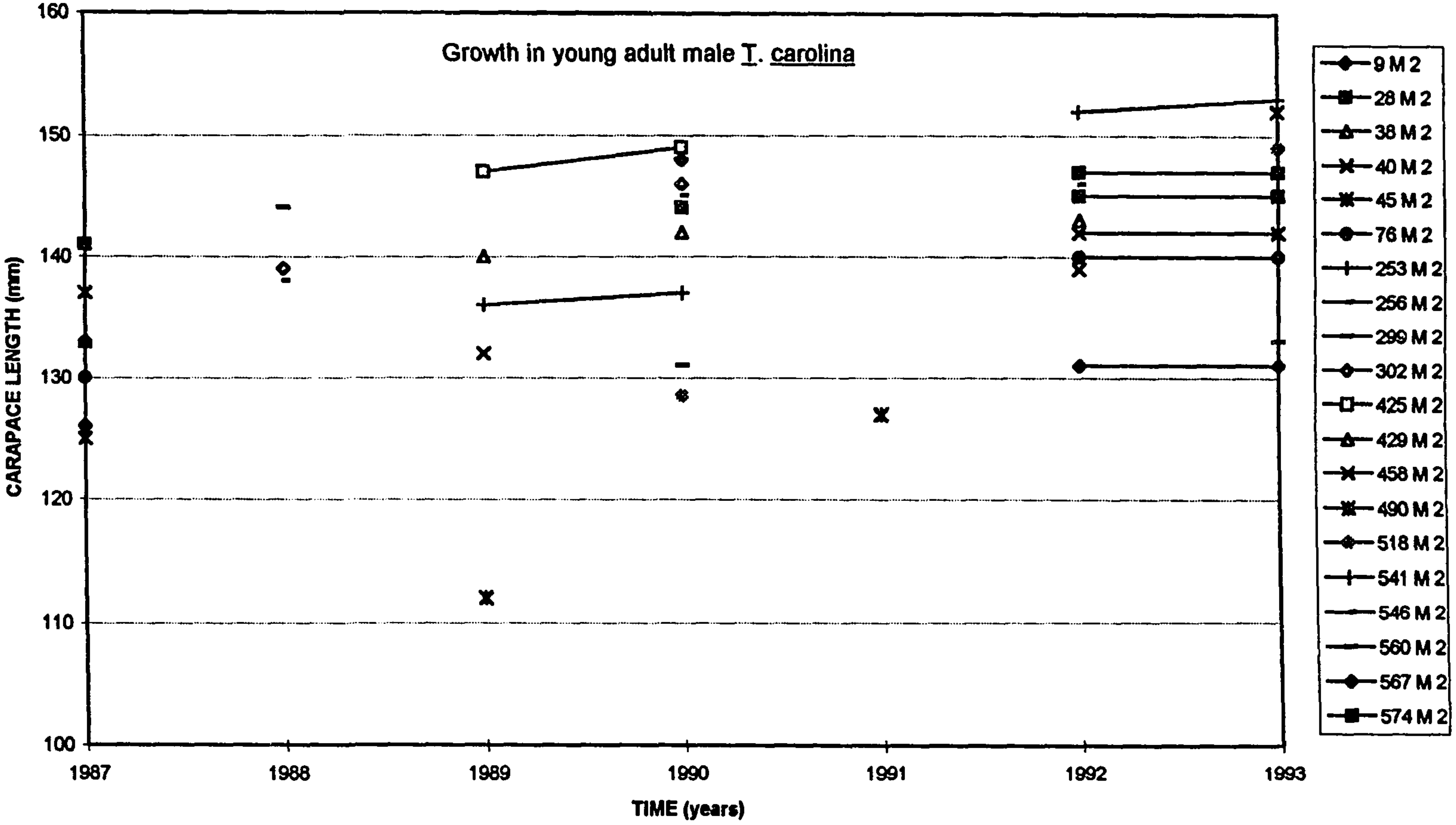

Figure 20. Carapace length growth (mm) in young adult (age class 2) male T. carolina repatriated to Floyd Bennett Field.

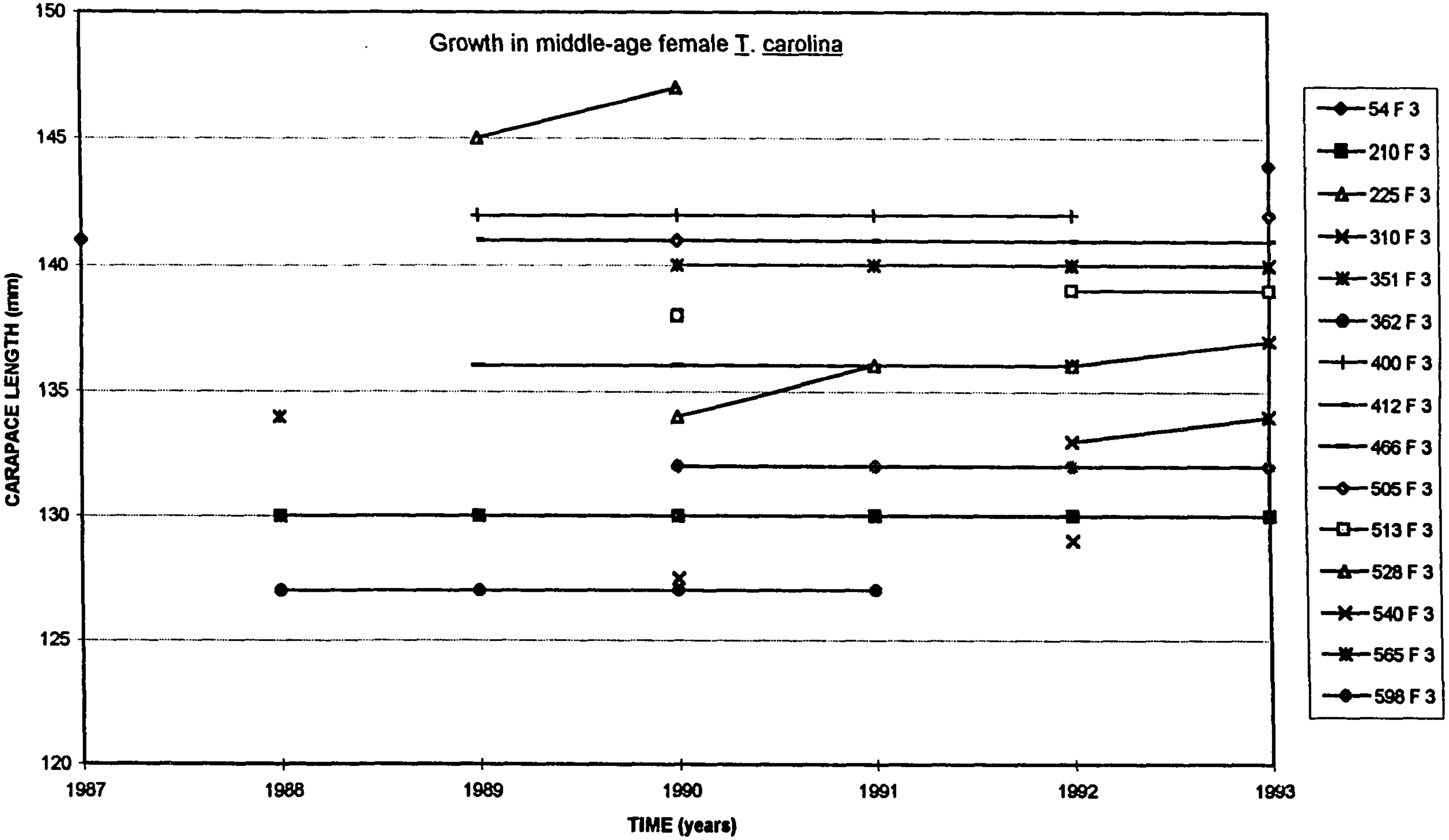

Figure 21. Carapace length growth (mm) in mid-age (age class 3) female T. carolina repatriated to Floyd Bennett Field.

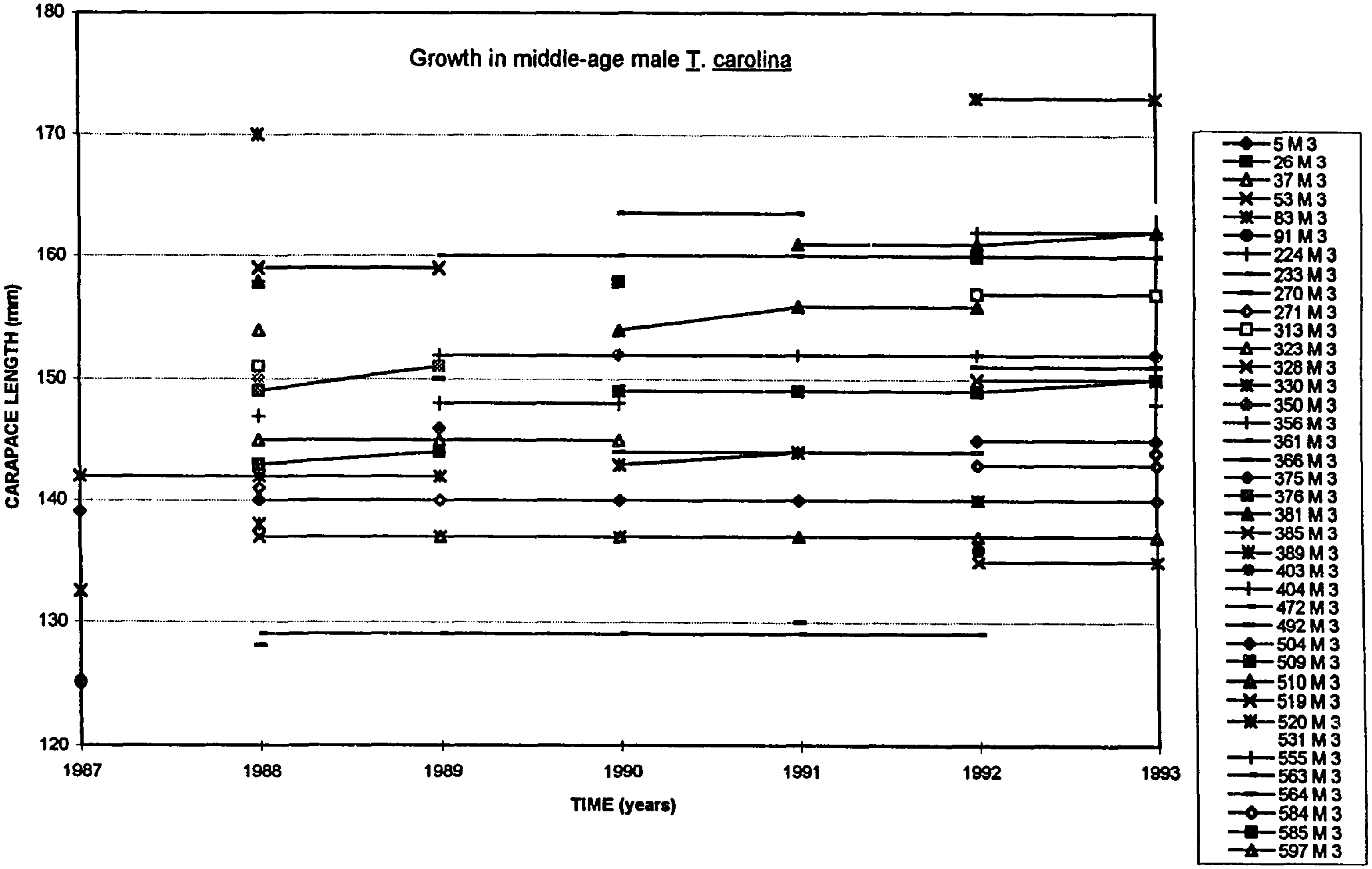

Figure 22. Carapace length growth (mm) in mid-age (age class 3) male T. carolina repatriated to Floyd Bennett Field.

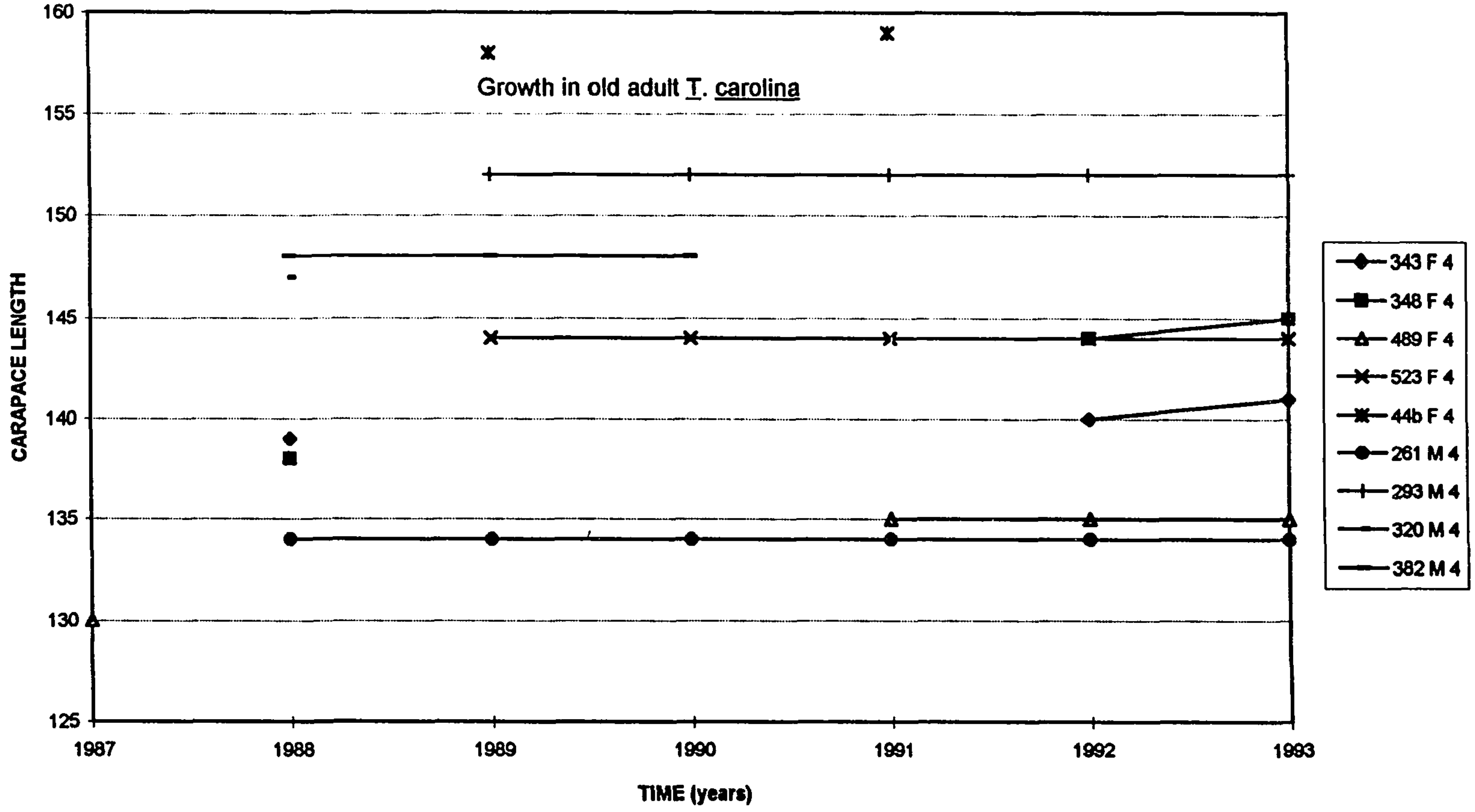

Figure 23. Carapace length growth (mm) in old adult (age class 4) T. carolina repatriated to Floyd Bennett Field.

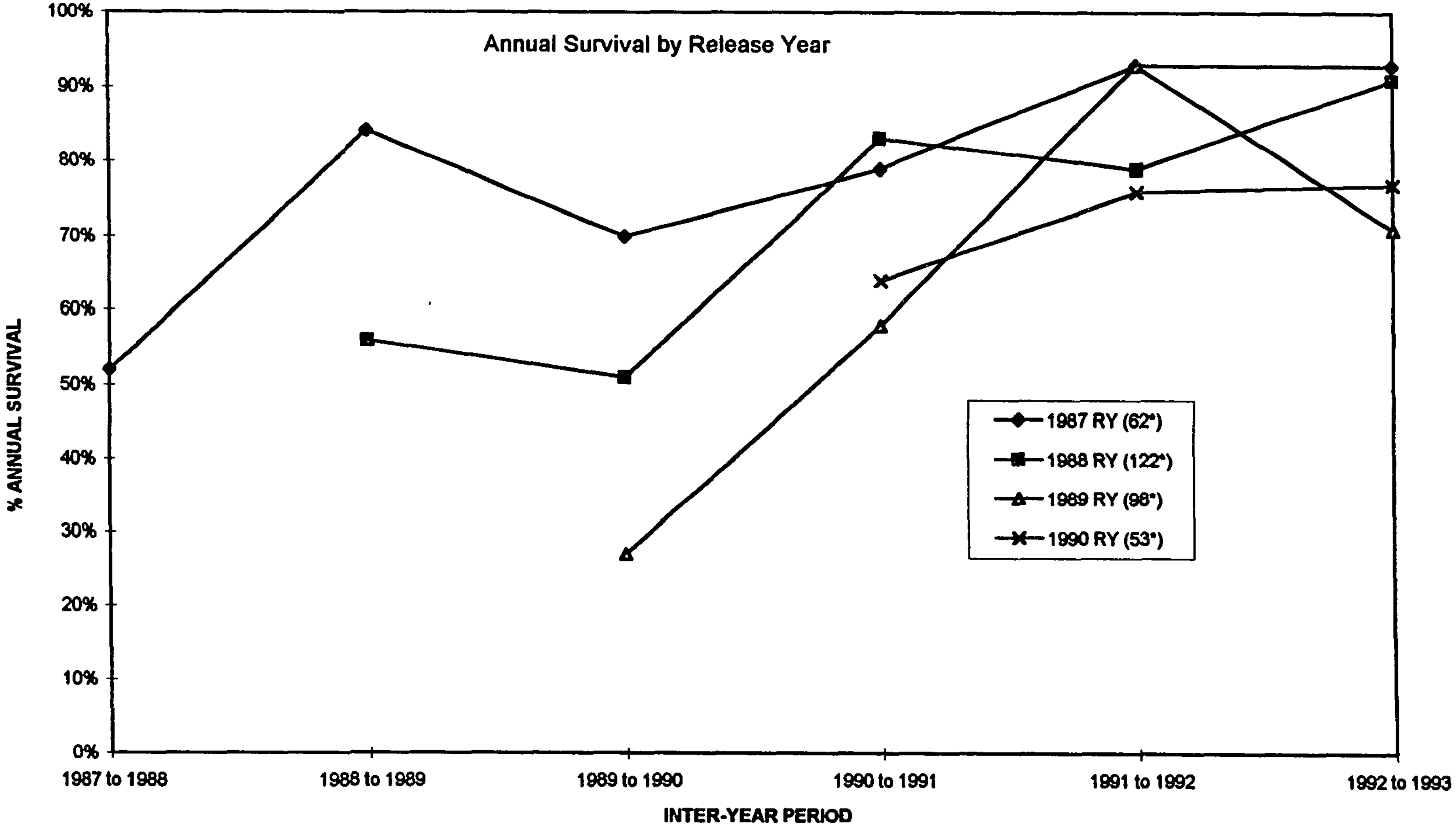

Figure 24. Annual survival by release year (RY) of all repatriated T. carolina (*=n).

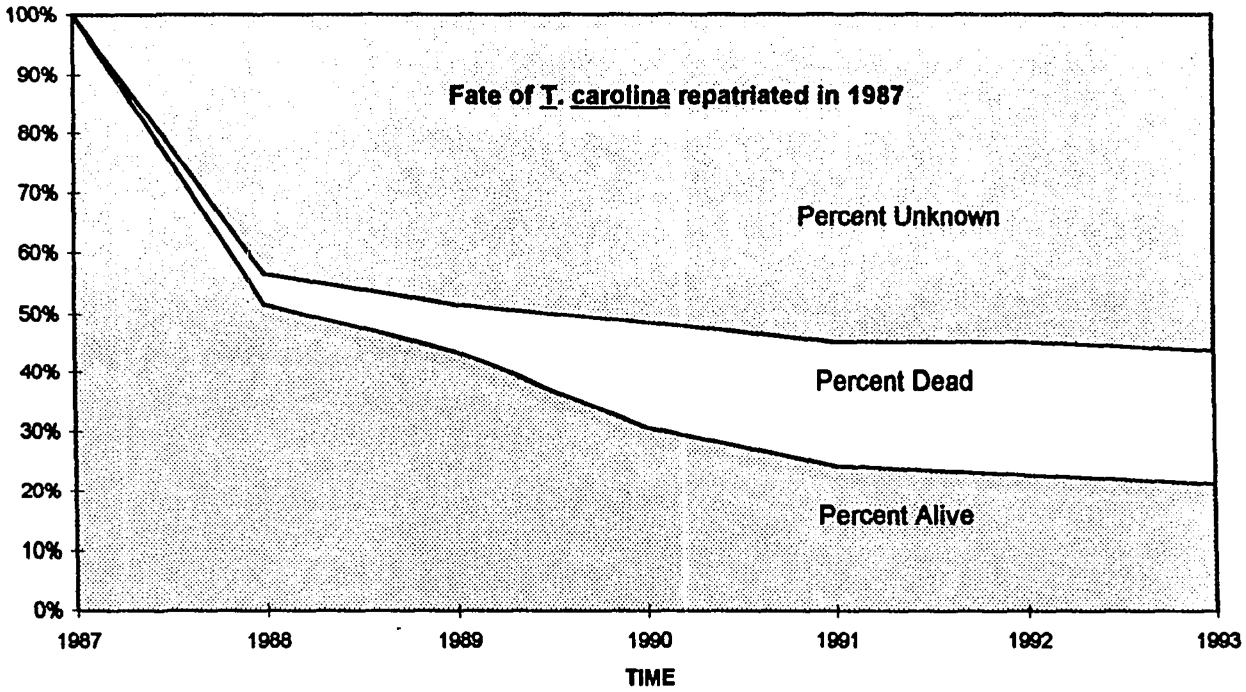

Figure 25. Fate of the 62 T. carolina repatriated to Floyd Bennett Field in 1987.

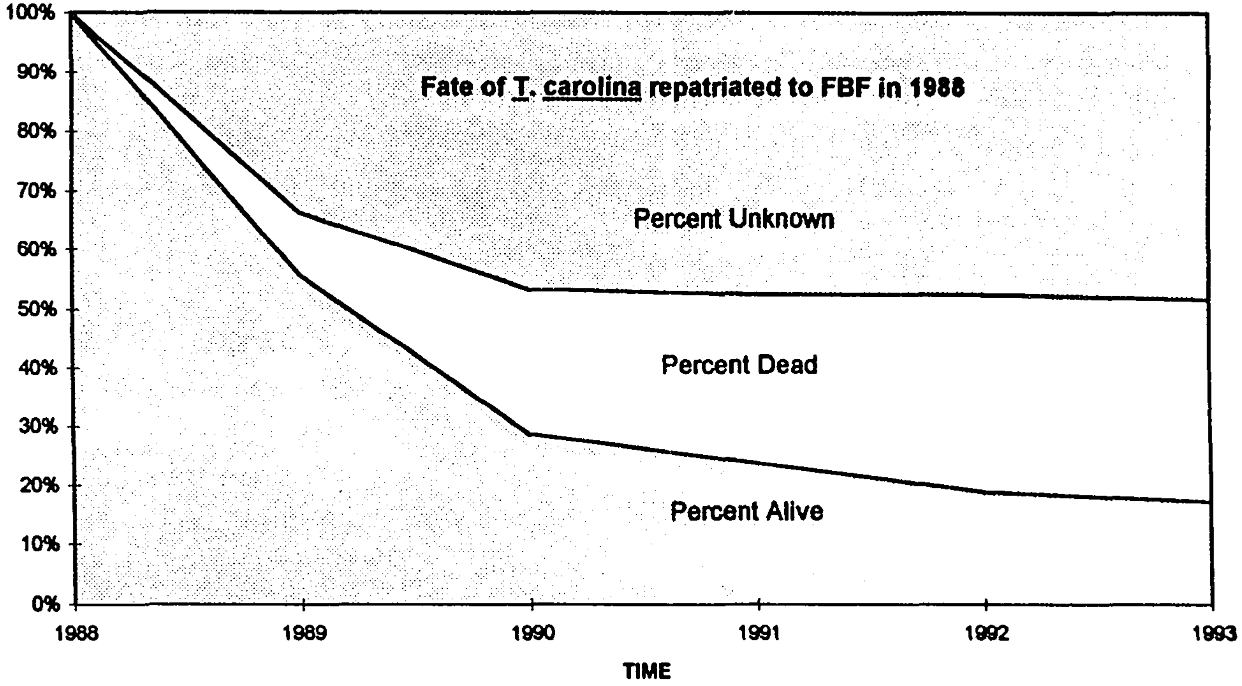

Figure 26. Fate of the 122 T. carolina repatriated to Floyd Bennett Field in 1988.

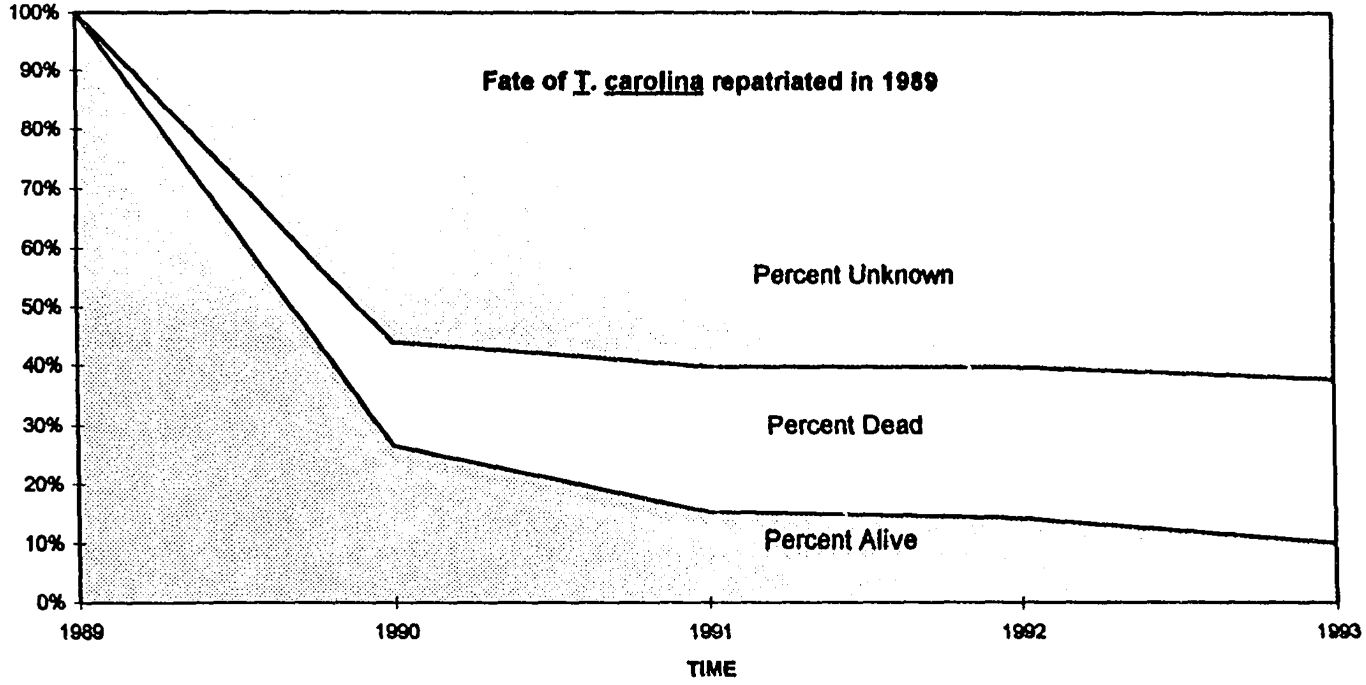

Figure 27. Fate of the 98 T. carolina repatriated to Floyd Bennett Field in 1989.

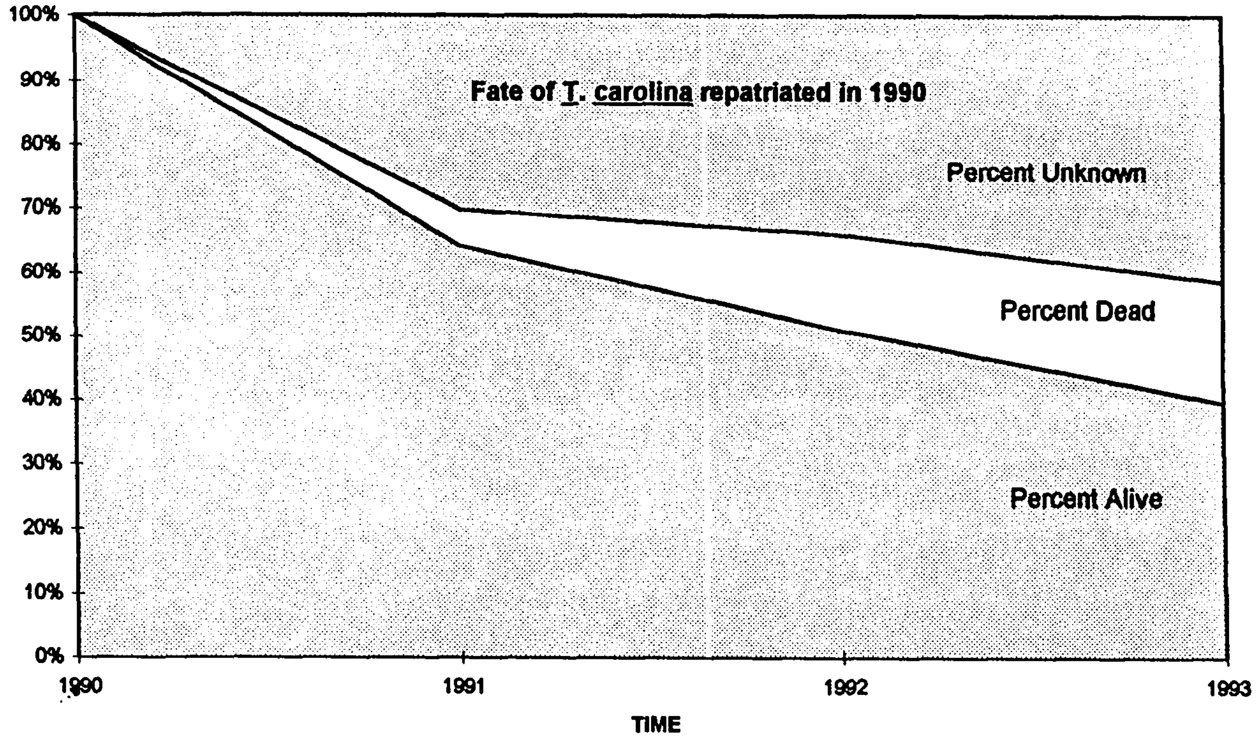

Figure 28. Fate of the 53 T. carolina repatriated to Floyd Bennett Field in 1990.

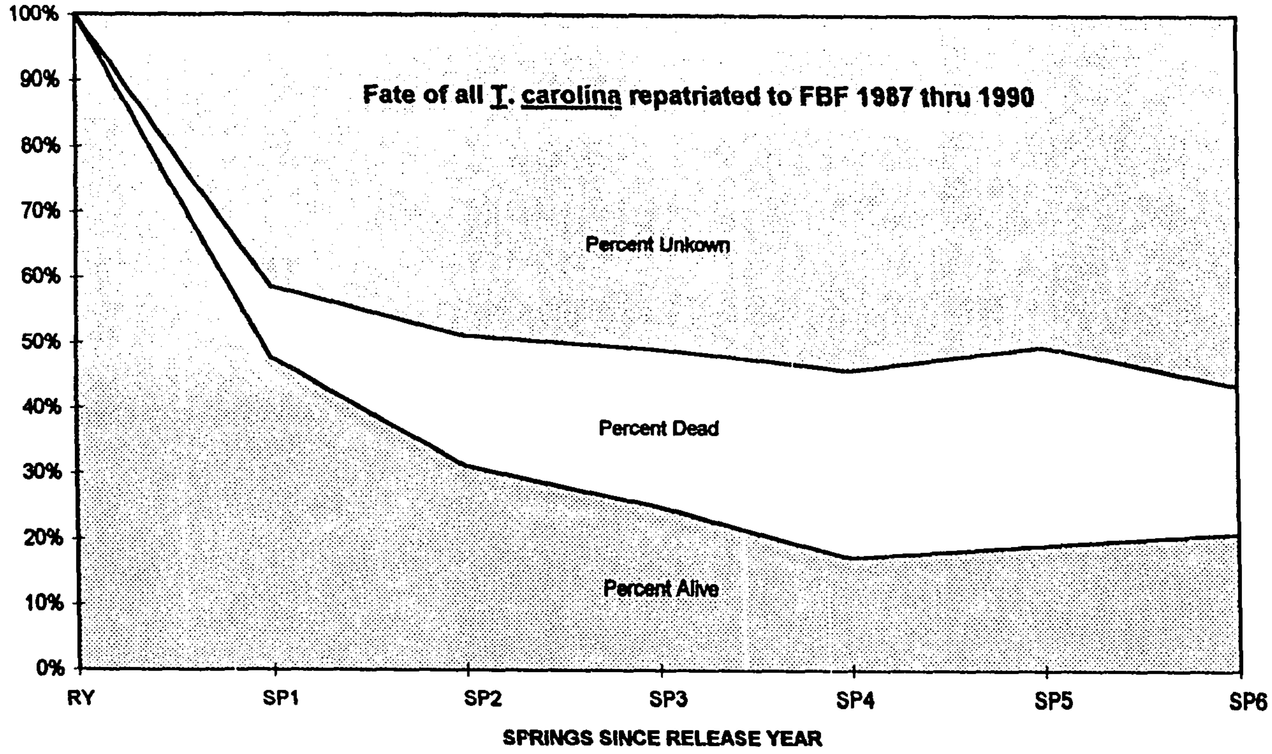

Figure 29. Fate of all T. carolina repatriated to Floyd Bennett Field. Time expressed as springs since release year (RY).

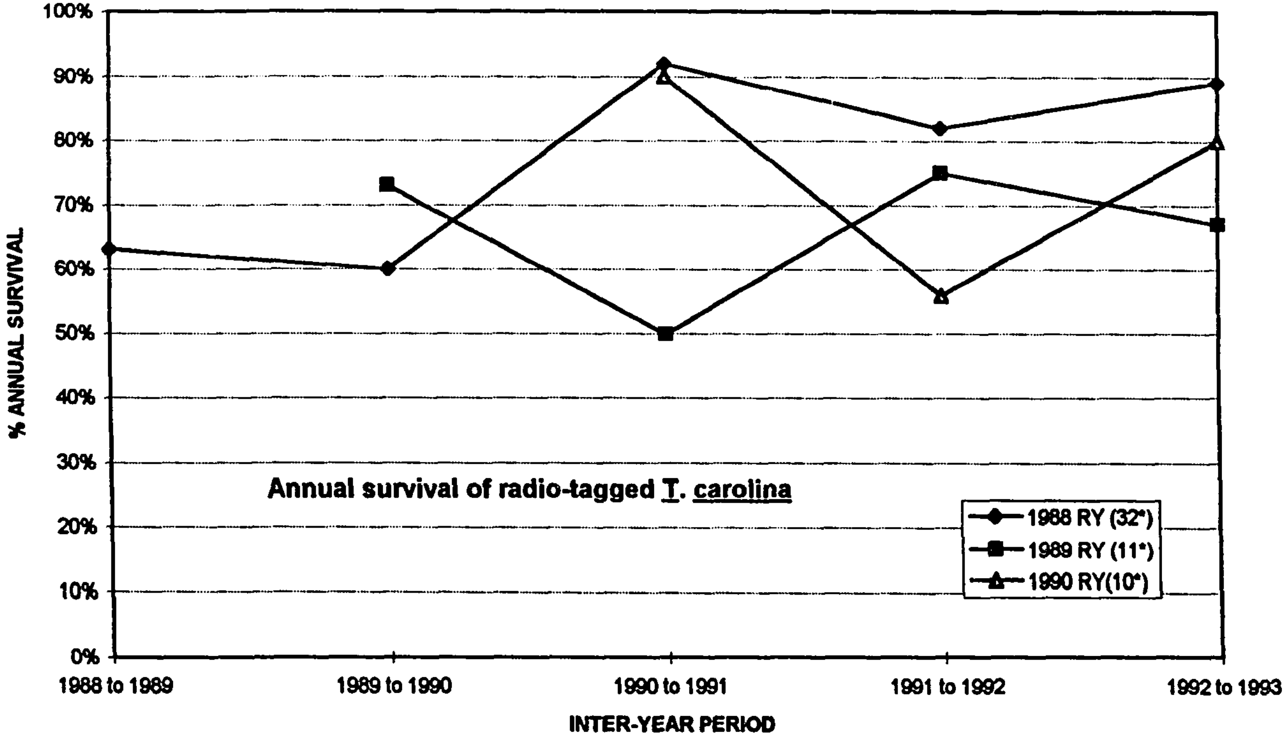

Figure 30. Annual survival of release year (RY) cohorts of repatriated <u>T</u>. <u>carolina</u> monitored by radio (*=n).

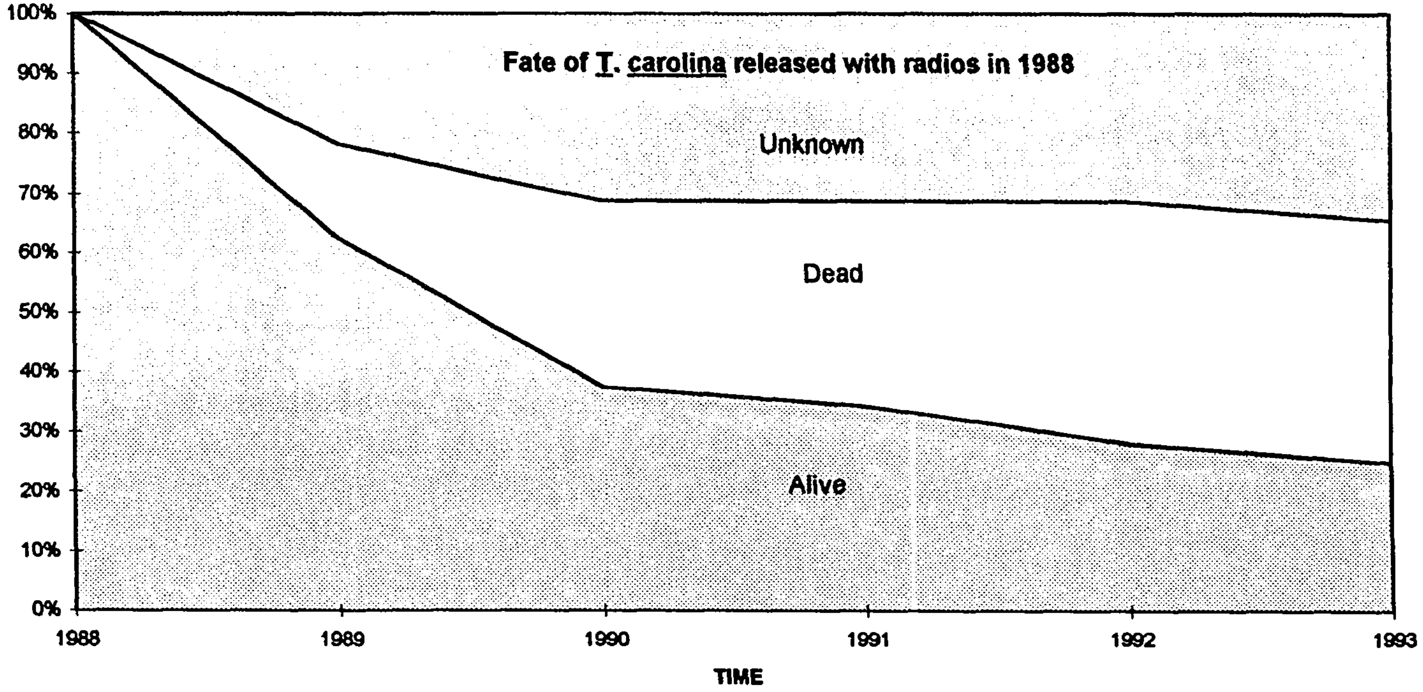

Figure 31. Fate of 32 T. carolina repatriated to Floyd Bennett Field in 1988 and radio-tracked.

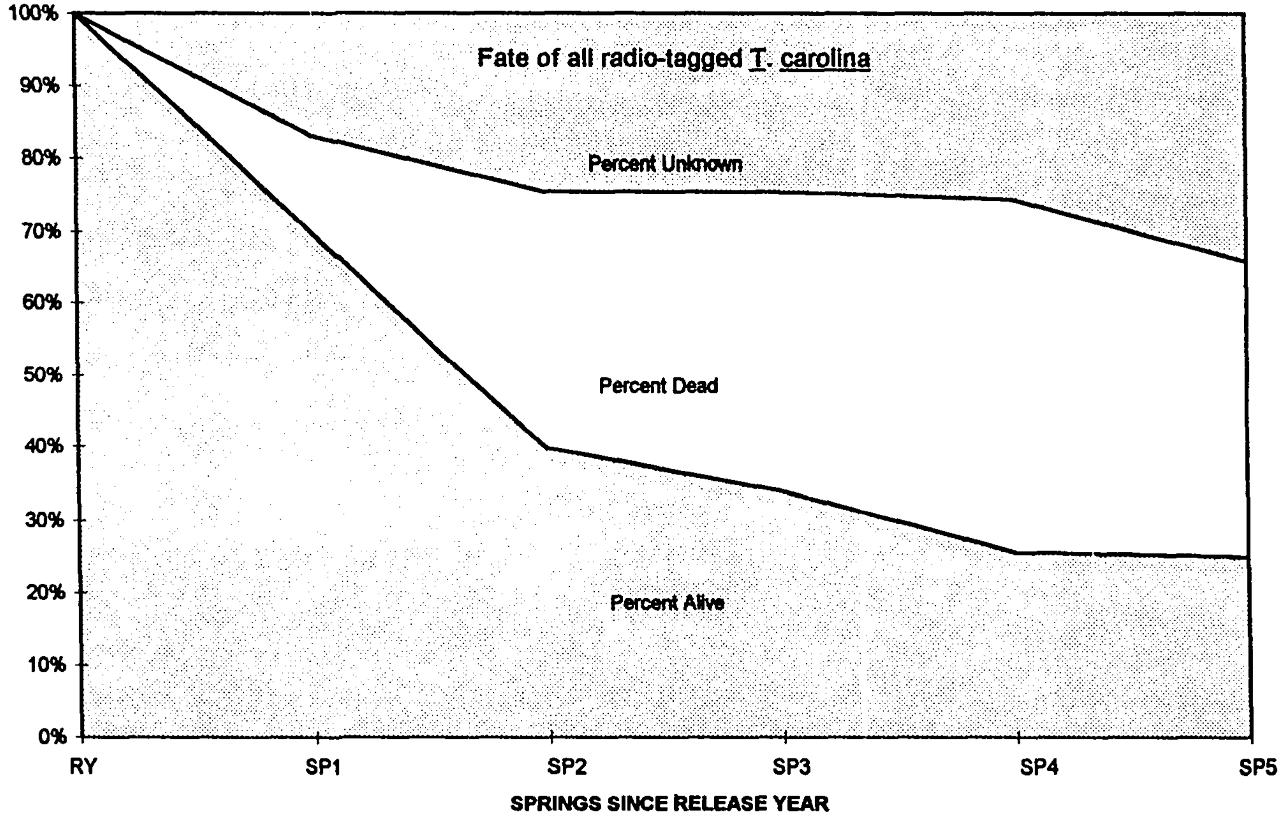

Figure 32. Fate of radio-tagged T. carolina repatriated to Floyd Bennett Field from 1988 to 1990. Time expressed as springs since release year.

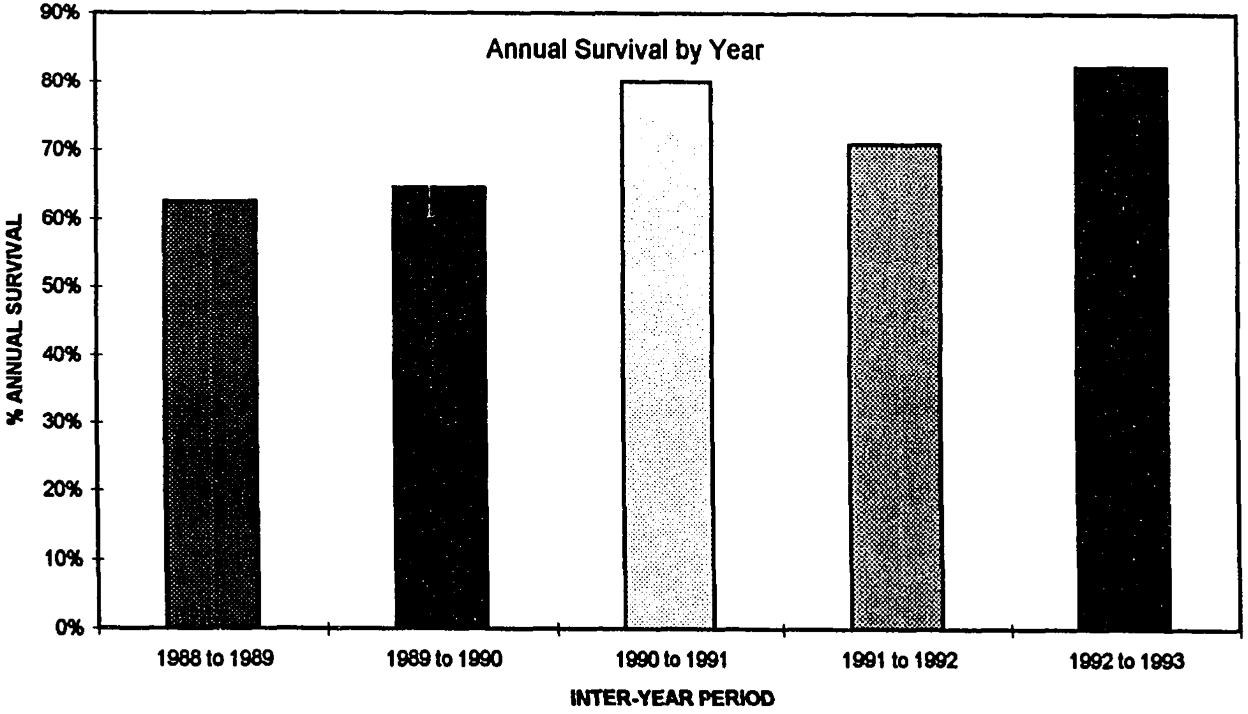

Figure 33. Annual survival by calender year of radio-tagged repatriated T. carolina.

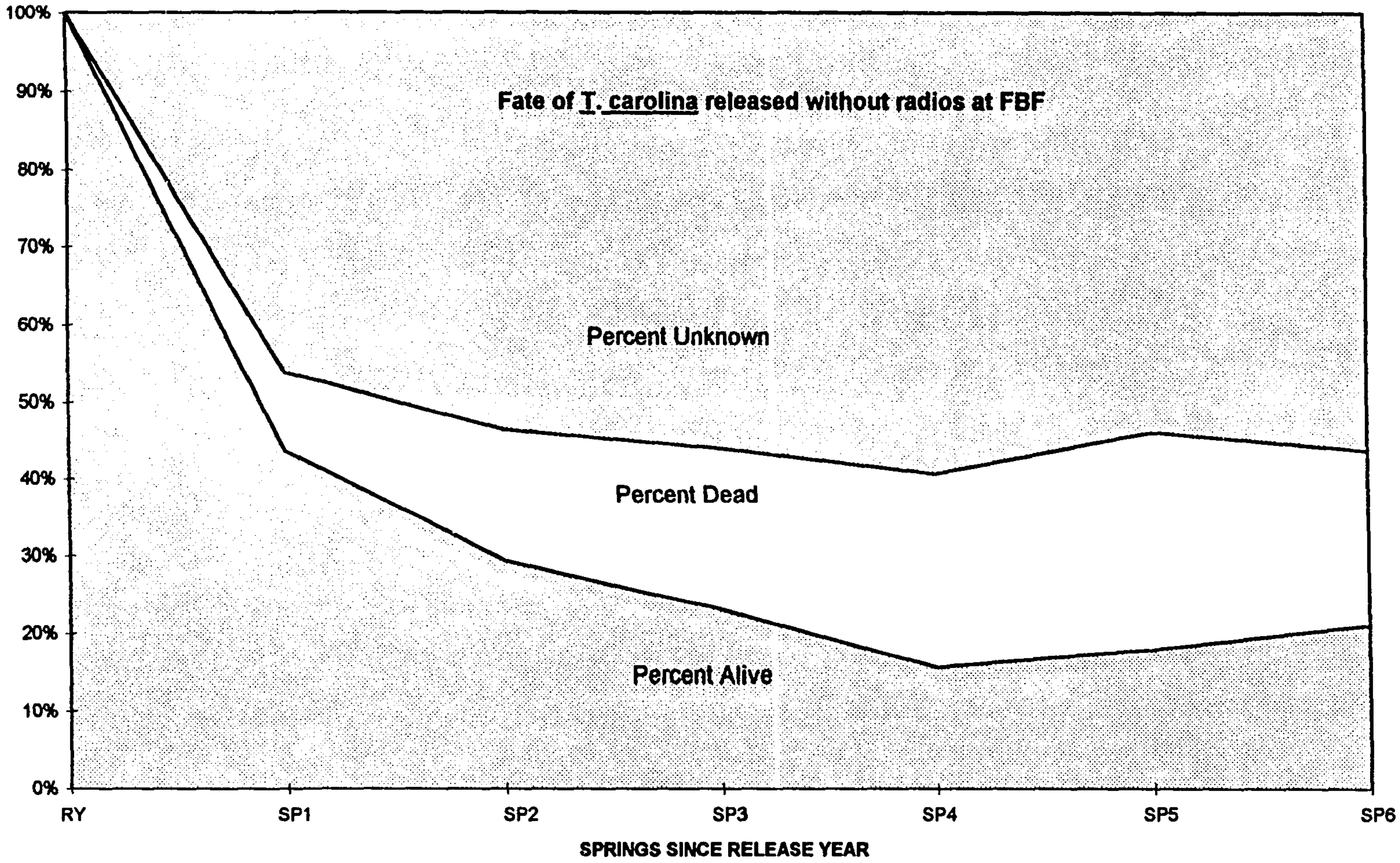

Figure 34. Fate of T. carolina released without radios. Time expressed as springs since release year.

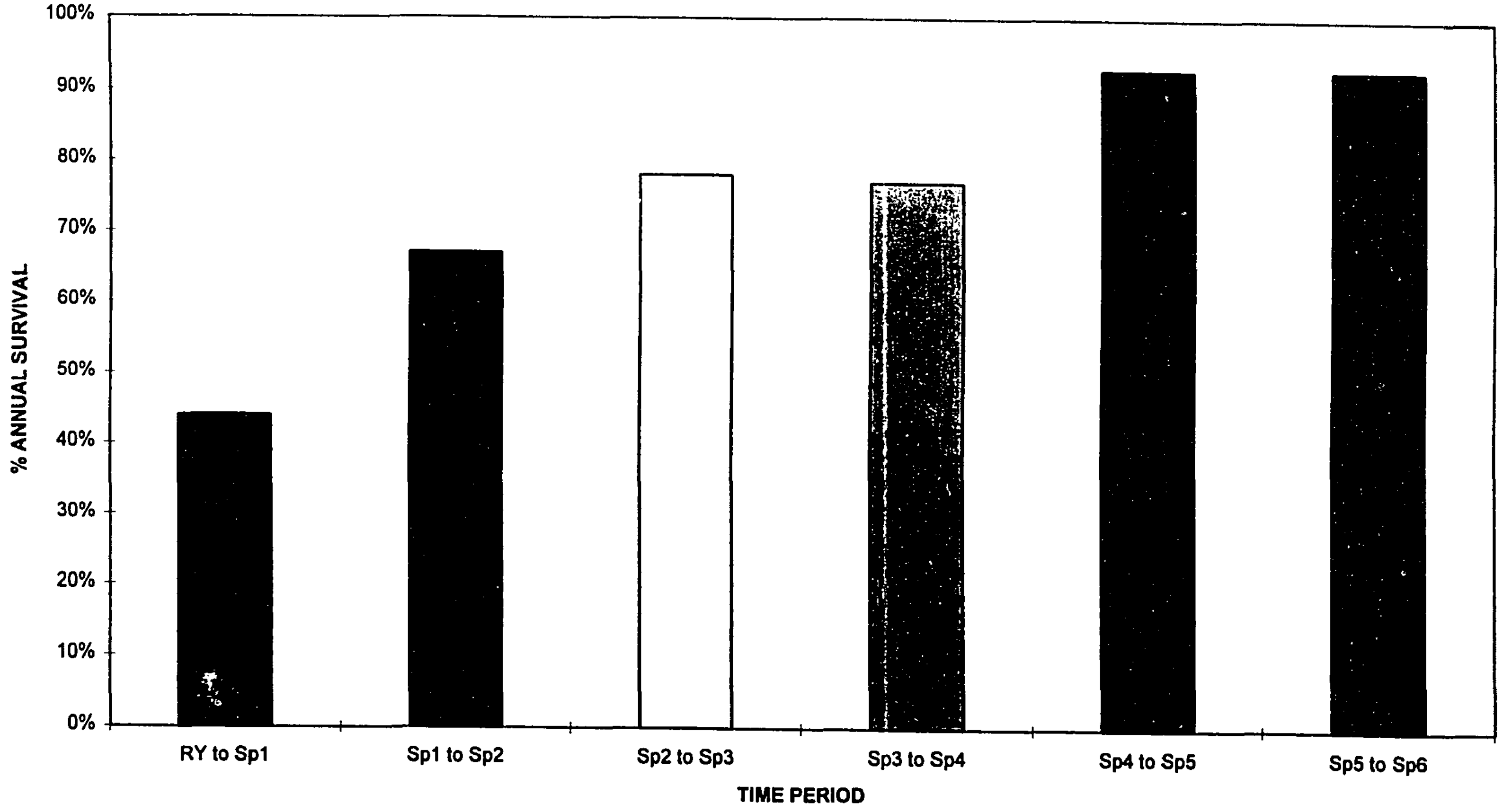

Figure 35. Annual survival of *T. carolina* released without radios. Time periods are from release year (RY) to first spring after release (Sp1) etc.

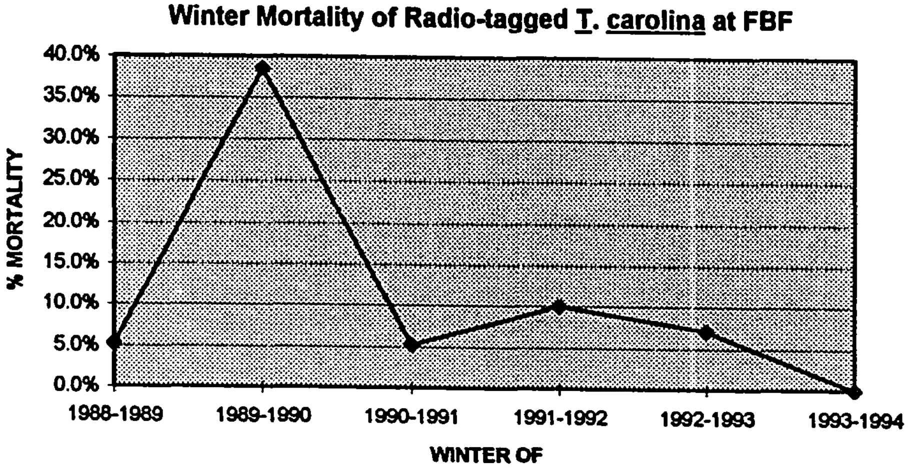

Figure 36. Winter mortality of radio-tagged T. carolina repatriated to Floyd Bennett Field.

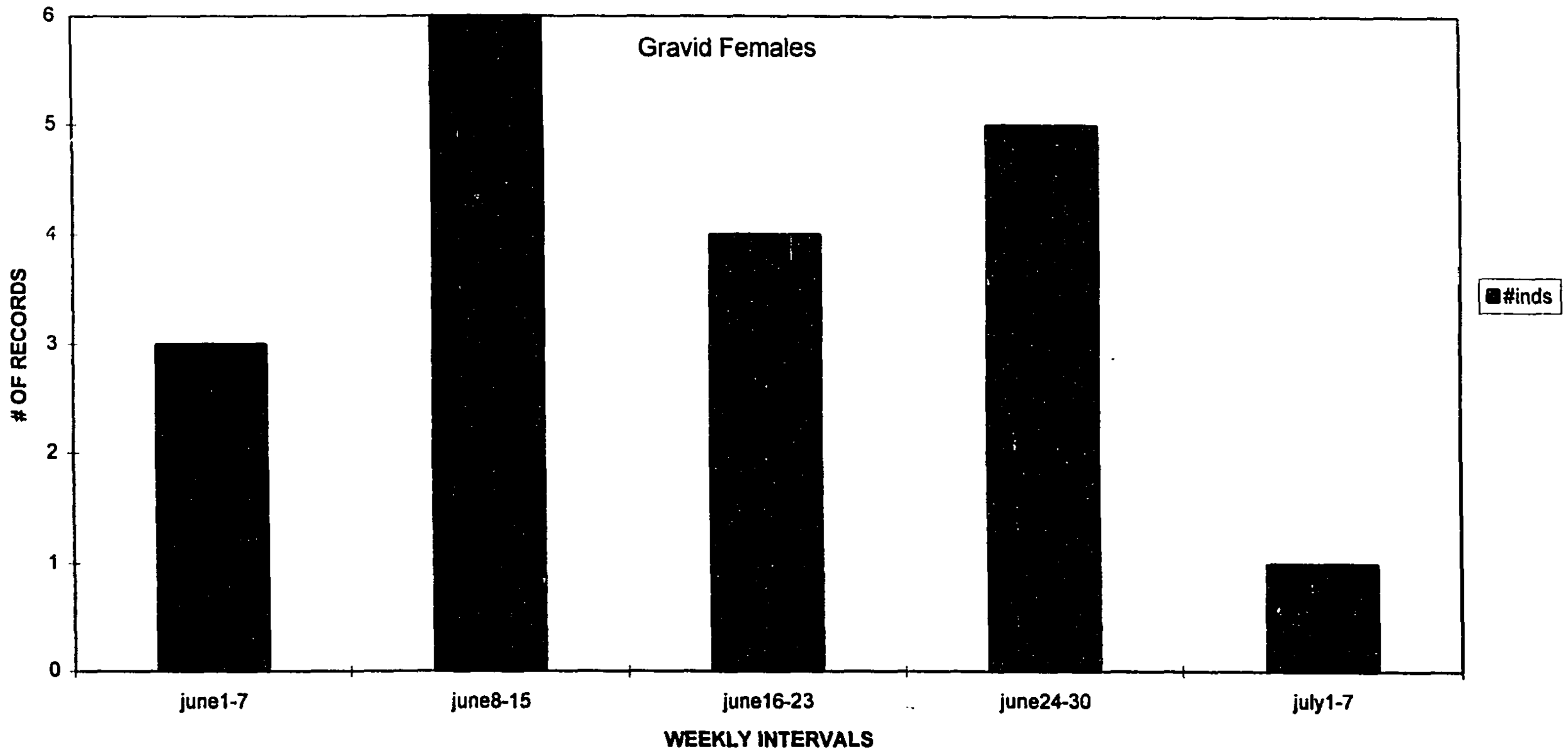

Figure 37. Distribution of dates when gravid female *T. carolina* were recorded on Floyd Bennett Field.

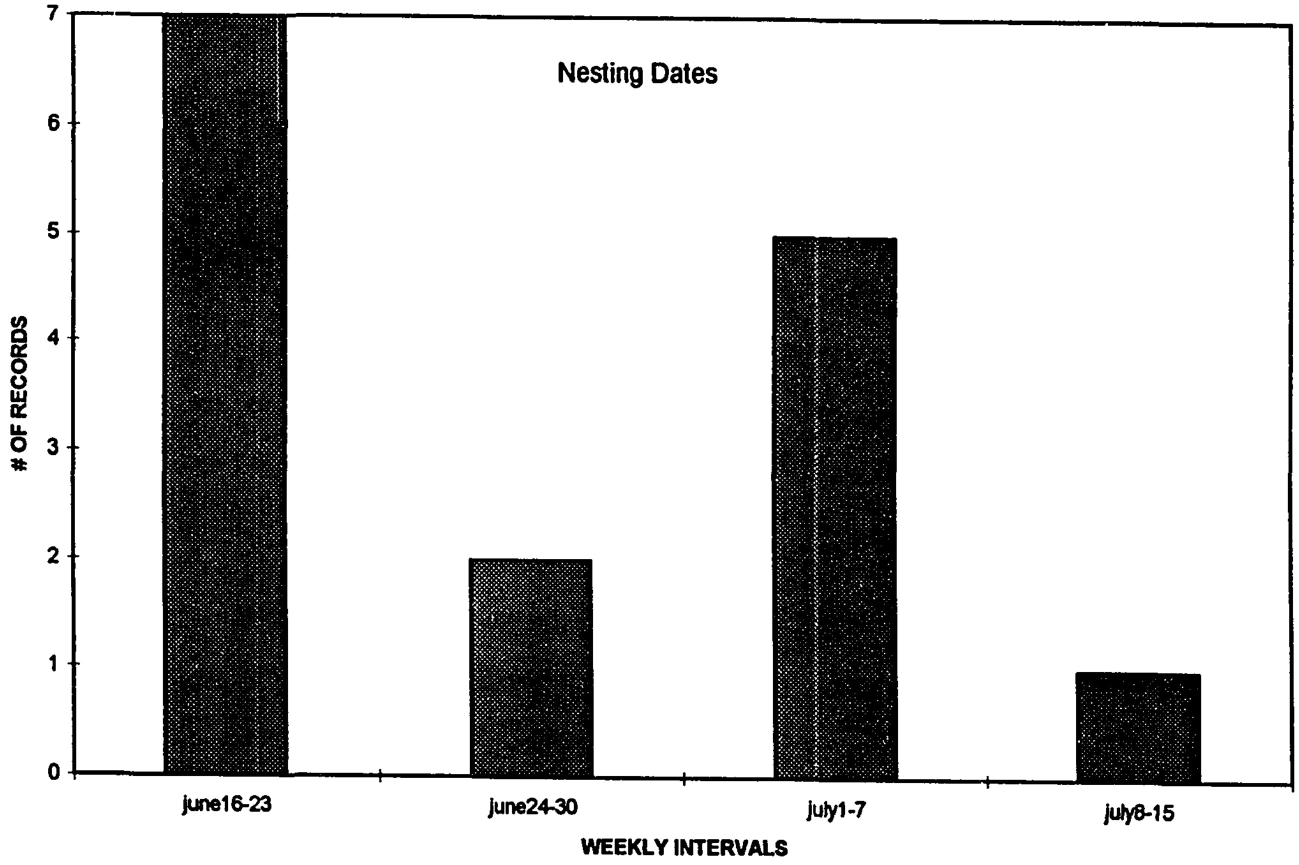

Figure 38. Estimated nesting dates of T. carolina at Floyd Bennett Field.

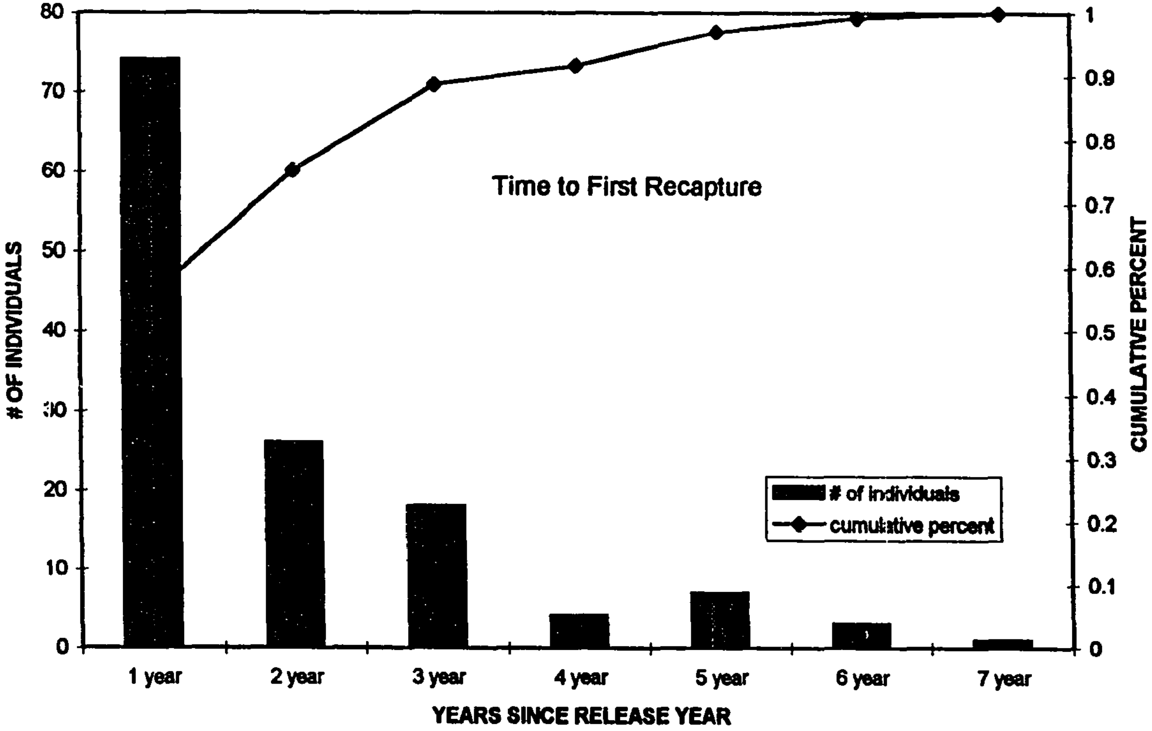

Figure 39. "Time to first long-term recapture" in T. carolina repatriated to Floyd Bennett Field and released without radios.

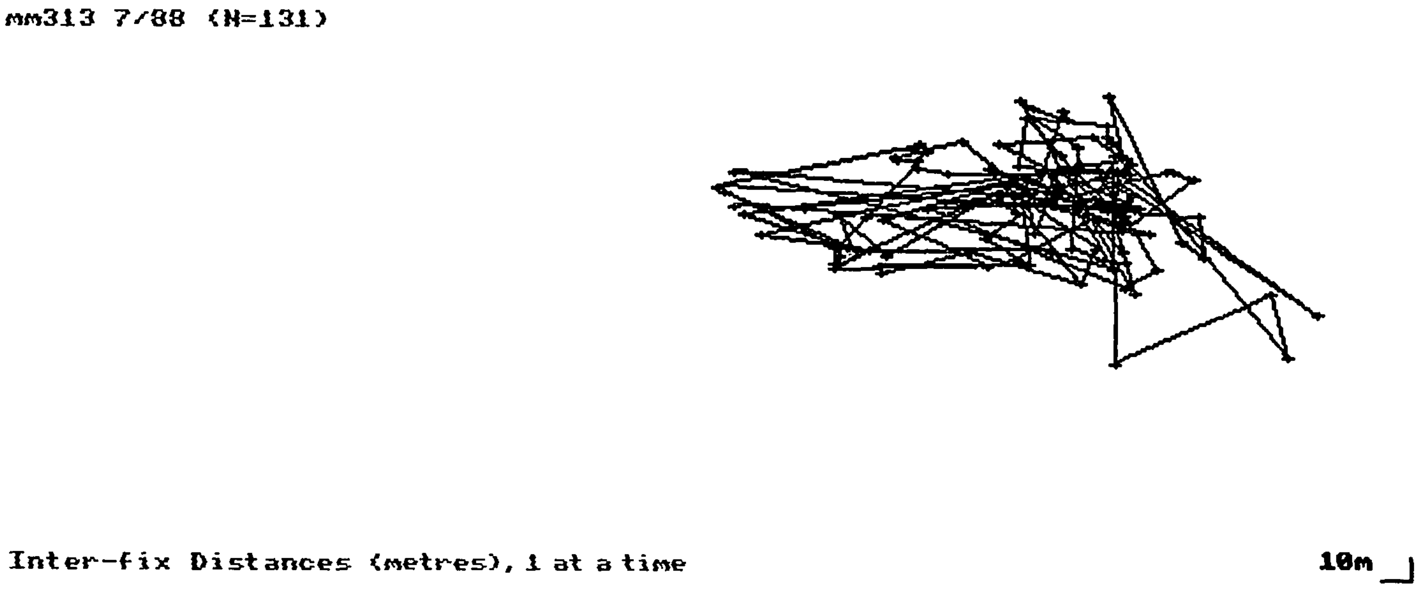

Figure 40. Movement by repatriated T. carolina #T313 (an individual whose home range included the release point {stippled}).

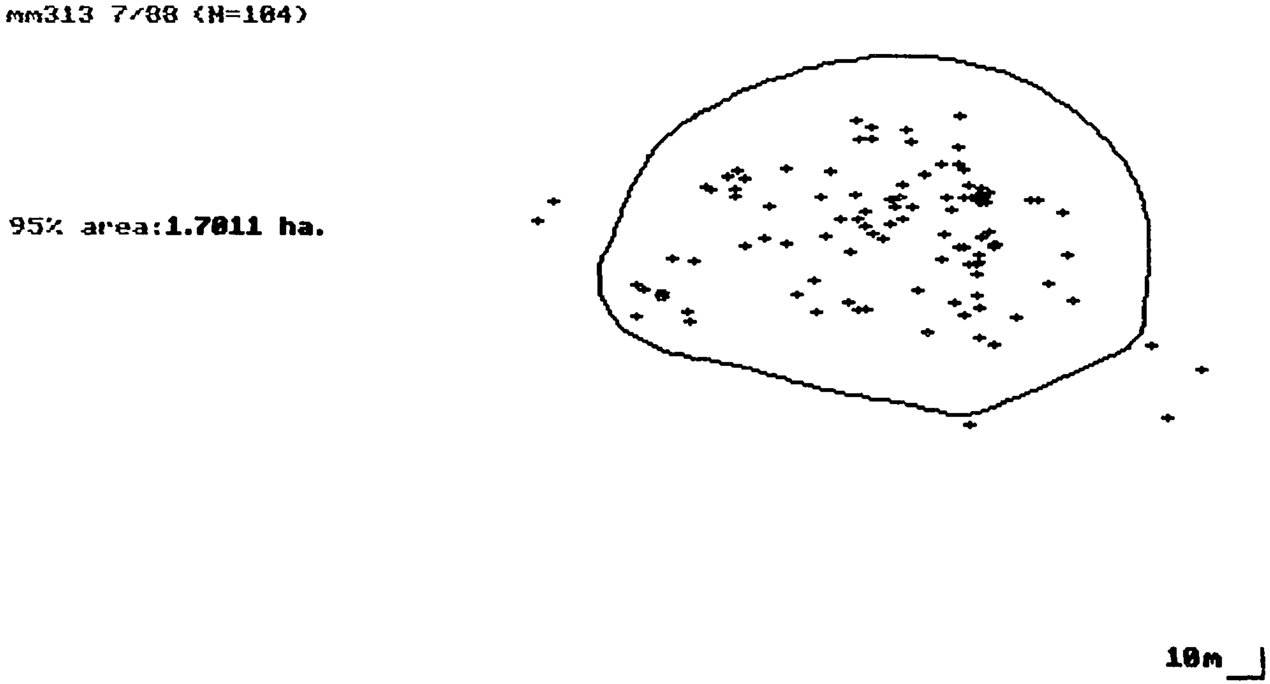

Figure 41. Locations and 95% harmonic mean home range for repatriated T. carolina . Home range includes release point (stippled). Large diamond is harmonic center.

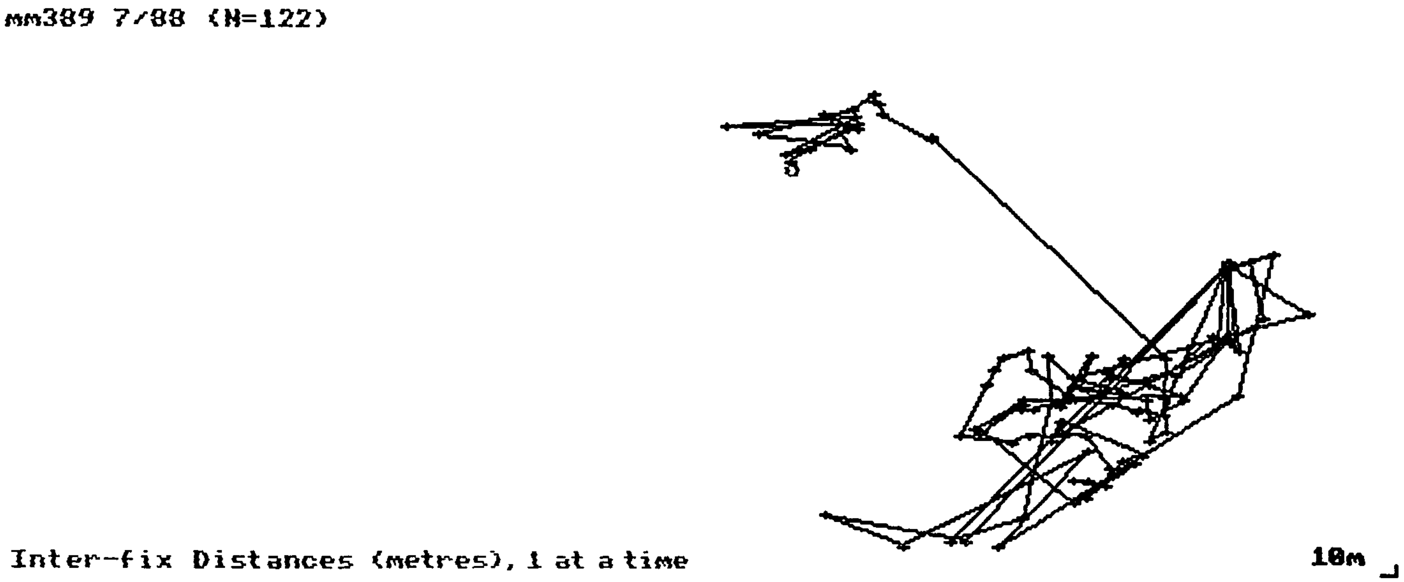

Figure 42. Movements of repatriated T. carolina #T389 (an individual who dispersed from the release point prior to home range establishment.. Release point shown as stippled oval.

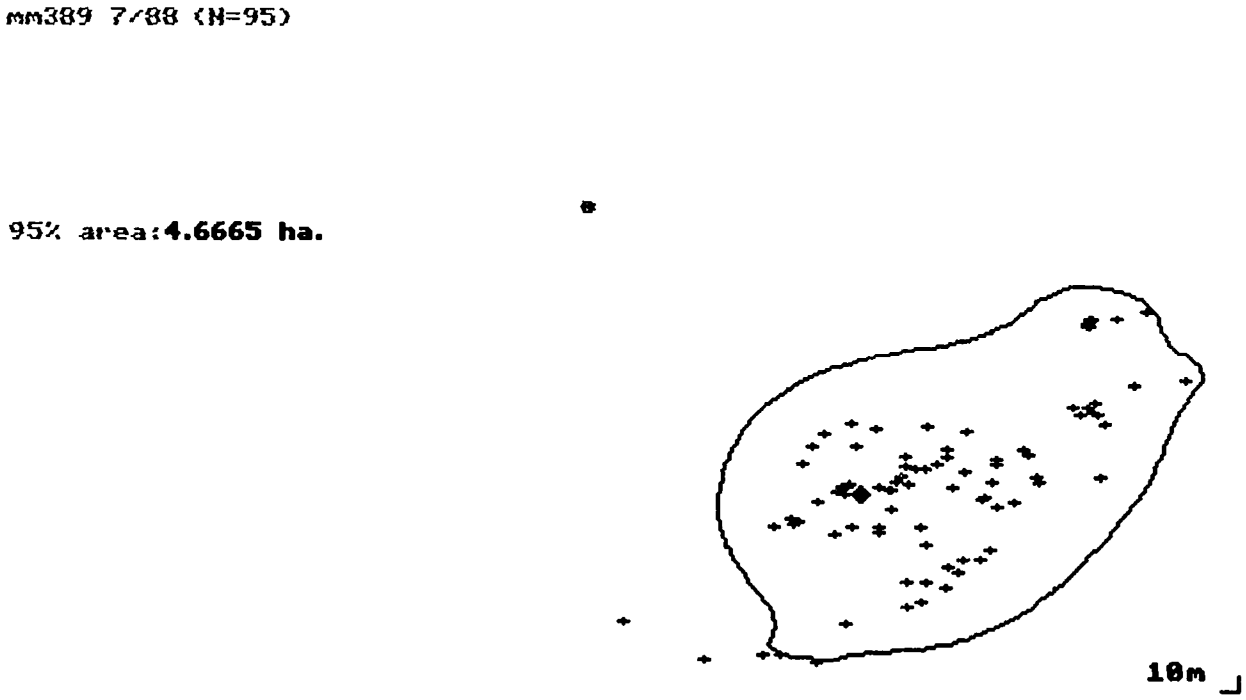

Figure 43. Locations and 95% harmonic mean home range for repatriated T. carolina #T389. Home range does not include release point (stippled). Large diamond is harmonic center.

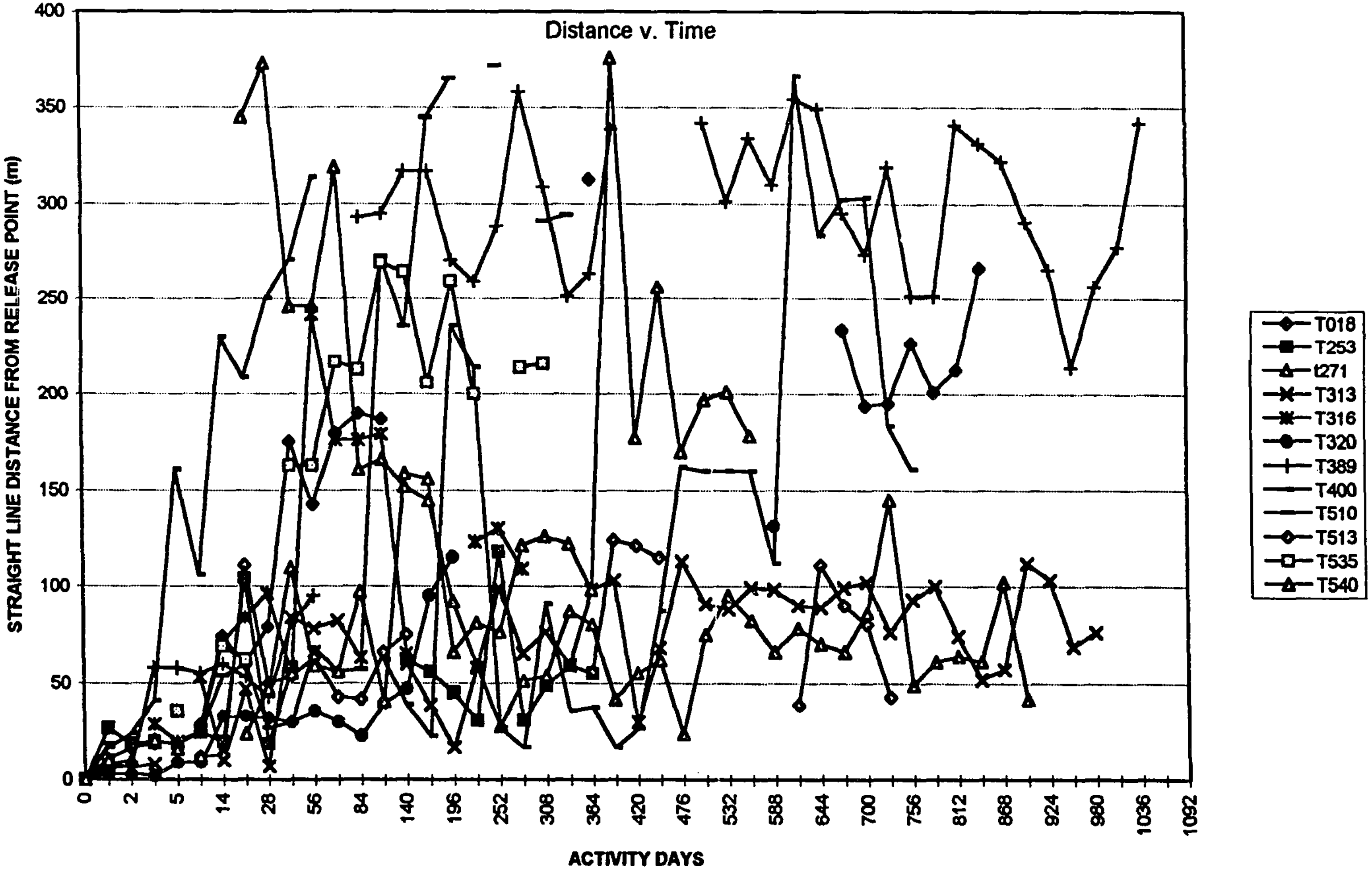

Figure 44. Straight-line distance from release point v. time for T. carolina that established home ranges <400 m from release point.

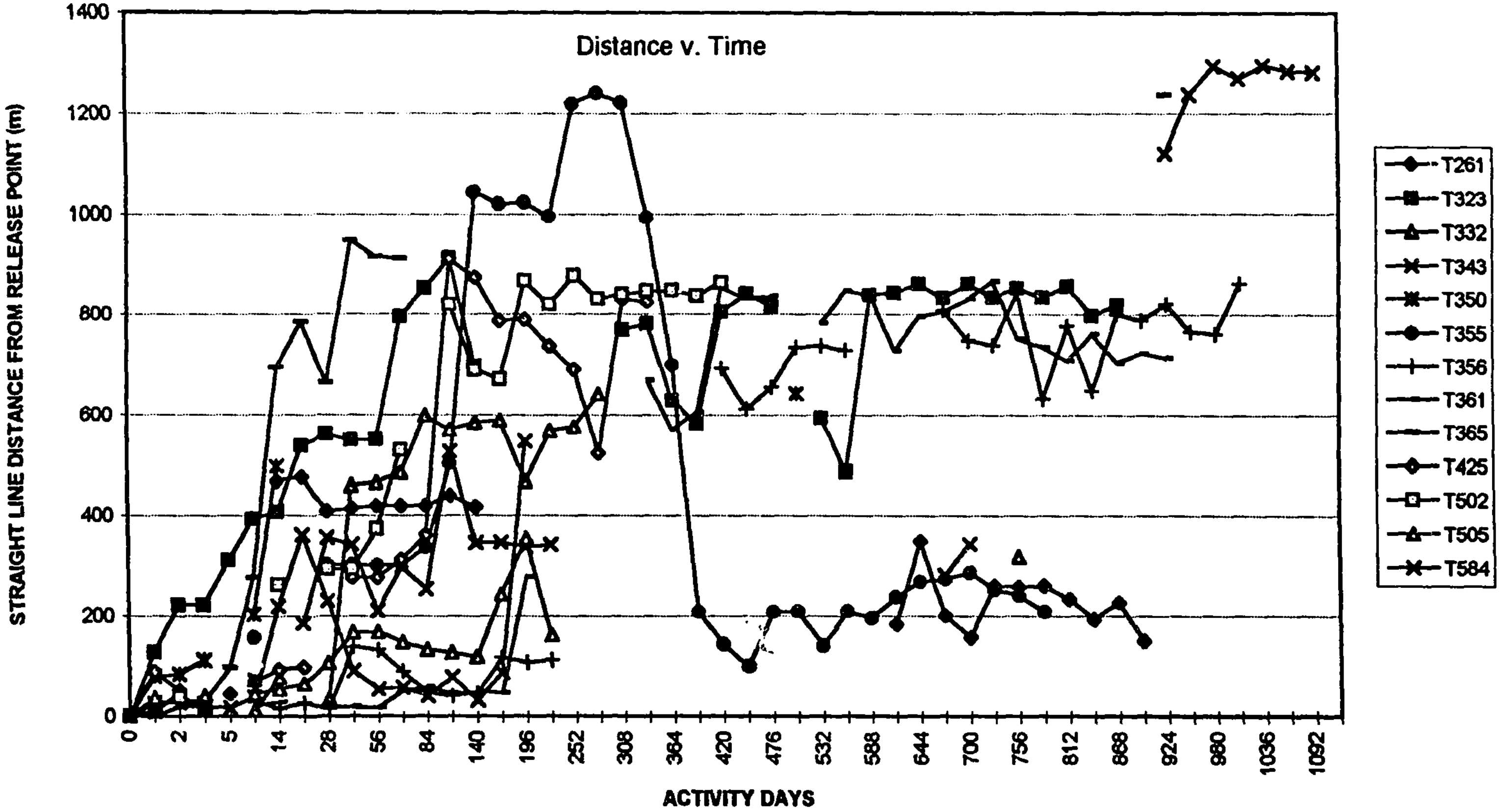

Figure 45. Straight-line distance from release point v. time for T. carolina that established home ranges >400 m from release point.

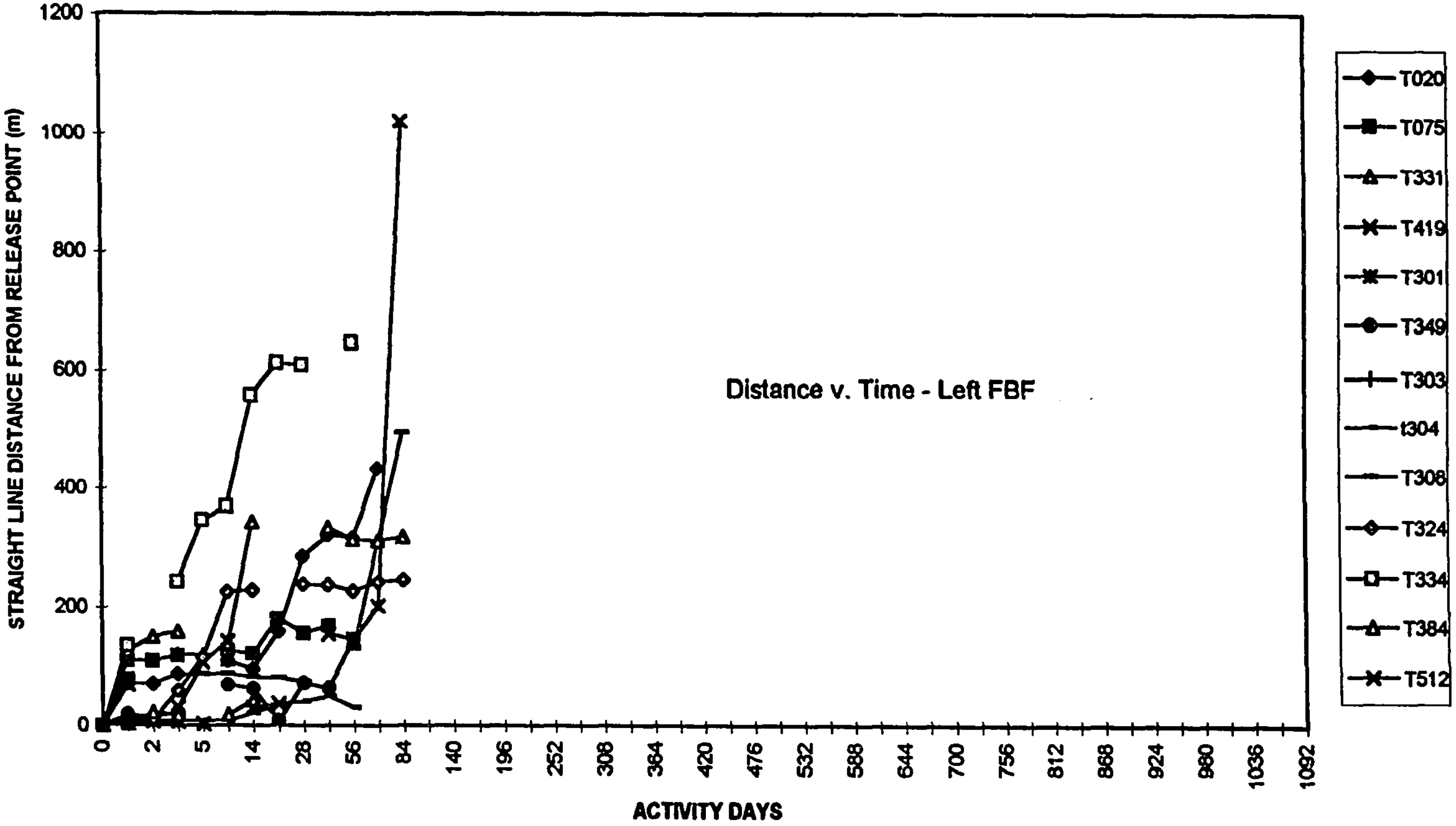

Figure 46. Straight-line distance from release point v. time for repatriated T. carolina that dispersed from Floyd Bennett Field.

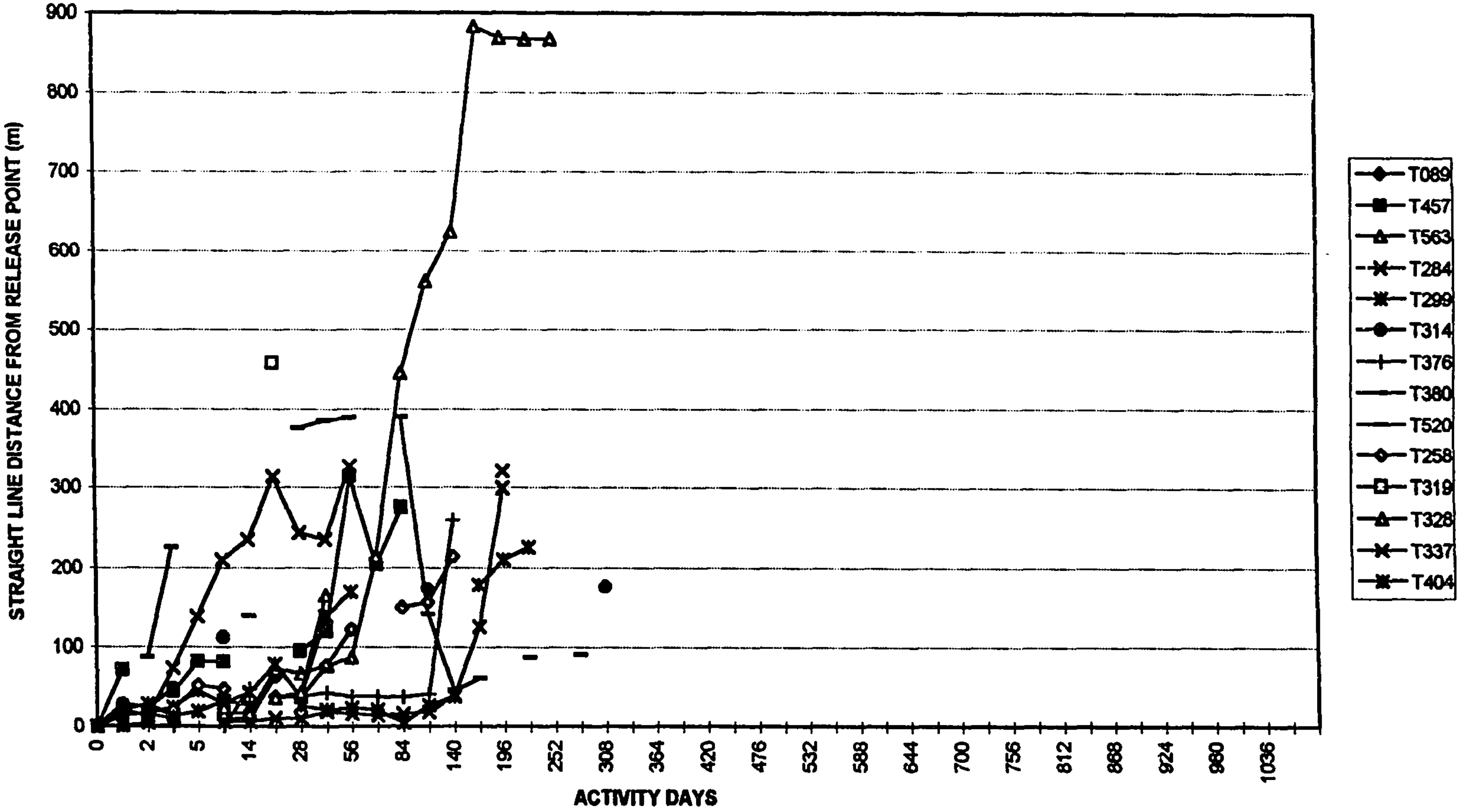

Figure 47. Distance from release point v. time for repatriated T. carolina that died before leaving site or establishing a home range.

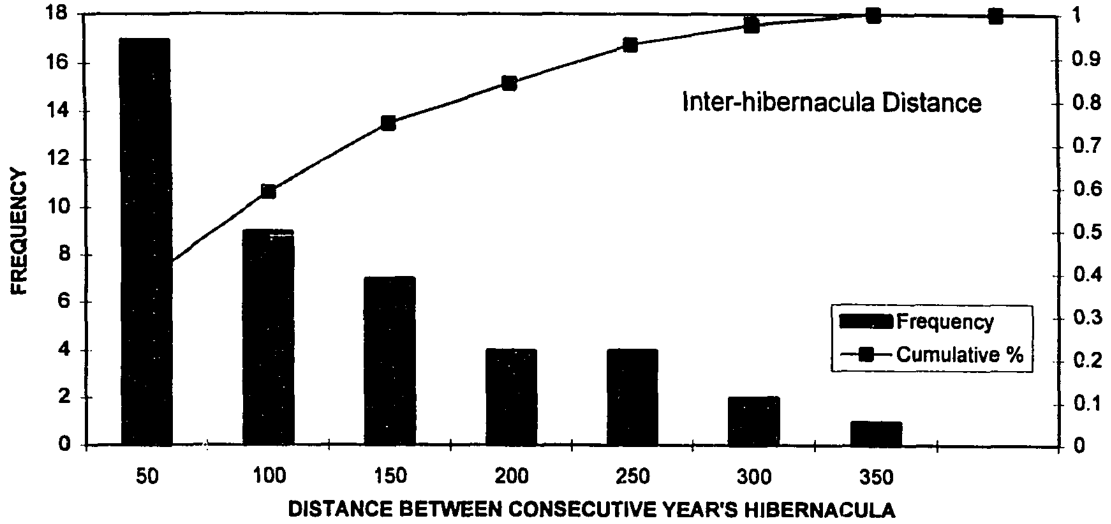

Figure 48. Frequency distribution of distance between consecutive year's hibernacula in T. carolina repatriated to Floyd Bennett Field.

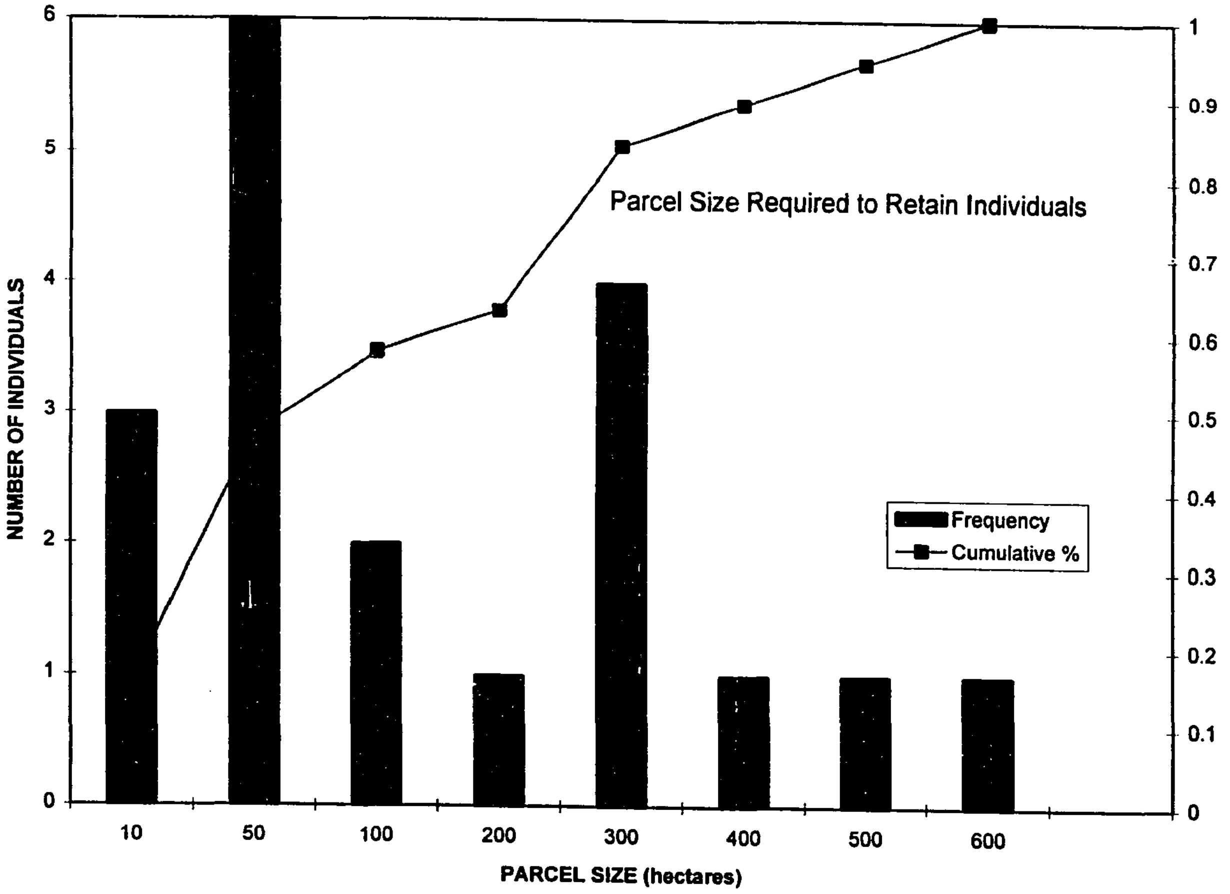

Figure 49. Frequency distribution of parcel size required to retain repatriated T. carolina. Based on maximum distance from release point and assumption of a circular area.

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