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Home Range of the Florida Red-Bellied Turtle (*Pseudemys nelsoni*) in a Florida Spring Run

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The home range of the Florida red-bellied turtle, *Pseudemys nelsoni*, in a Florida spring run is described using both maximum distance over water and Ford and Krumme's (1979) technique for producing a "composite" home range. Ford and Krumme's (1979) technique was also used to find the probabilities of capture/relocation within the composite home range. Spatial positions in the river were based on underwater captures/relocations and basking relocations. The results from both methods suggest that individuals at this study site use a small home range, on the order of 120 m in length, with no sex differences. These results are constrasted with those for *P. floridana* at the same site and with telemetry-generated data for *P. nelsoni* in a shallow lake in Paynes Prairie, Florida. Sympatric *P. floridana* appear to have larger home ranges, with a patchier distribution of nonzero capture/relocation probabilities. Estimates of the home-range areas of *P. nelsoni* in the lake are an order of magnitude larger than those in the run, perhaps due to more dispersed resources or the use of telemetry for relocating animals.

HOME range, "that area traversed by the individual in its normal activities of food gathering, mating and caring for young" (Burt 1943:351), is a standard ecological parameter. There are several methods for modeling home range which yield various shapes from which size may be calculated. These shapes include circles, ellipses, and various types of polygons (Anderson, 1982). Assessing use of the bounded area is also important (Jorgensen and Tanner, 1963), since use may reflect the distribution of resources within the home range. Home range use or utilization distribution can be calculated for an individual if it is relocated sufficiently often or, if the number of relocations per individual is small, averaged over many individuals using a mathematical technique (e.g., Ford and Krumme, 1979). The home-range size of semiaquatic turtles has often been estimated using the minimum convex polygon technique (Southwood, 1966) or Sexton's (1959:137–138)

definition, the "minimum direct distance over water between the two most distant points of capture." The latter is especially useful for turtles inhabiting rivers or streams.

Here I describe the home-range size and use of the Florida red-bellied turtle, *Pseudemys nelsoni*, in a small river, drawing on both Sexton's (1959) definition and the technique outlined in Ford and Krumme (1979). The latter technique possesses two distinct advantages for a data set with many individuals but few relocations per individual. First, a "composite" home range, using all the data from all the individuals, can be constructed. The composite home range can be considered as an alternative way of averaging relocation information from many individuals. Second, the probability of capture/relocation within the composite home range is found and can be interpreted as home-range use. This is the first report on home-range size for this species, and it is also the first time Ford and

Krumme's (1979) technique has been applied to animals largely restricted to up- or downstream movements. Certain advantages exist when working with a system of lower dimension; fewer data are necessary, and selecting appropriate values to start the computer's search for a solution appears to be less critical. Data collected on penninsular cooters (*P. floridana*) inhabiting the same part of the river, and for radio-tracked *P. nelsoni* inhabiting a small lake, are included for comparison.

MATERIALS AND METHODS

The main study site comprised a 980-m section of Rock Springs Run with an average width of about 30 m, located 2 km downstream from Rock Springs, Apopka, Orange County, Florida. Adult *P. nelsoni* and *P. floridana* were captured indiscriminately by hand underwater and, after measuring and marking, released near the point of capture. A number was painted on the carapace in four places with rubberized or epoxy paint. The painted number was discernable for one to three months. Animals were also marked more permanently by drilling one to three small holes in the first three or last five marginals (Cagle, 1939) and inserting a small plastic fabric tag. The tags remained in place for about one year. Because the holes often became obscured by algae, the tags proved useful in identifying marked animals seen but not recaptured later.

The study was conducted intermittently during a three-year period (1983–1985). Animals were marked only in the first few days of each approximately one-month study period. Somewhat more time was spent collecting turtles in areas where they appeared to be more abundant; thus, capture effort was not equal throughout the study site. Animals were relocated during censusing of basking animals, during underwater behavioral observations, from a canoe when moving about the study area, and during underwater weekly searches throughout the study area. At the end of each study period, I searched approximately one km of the adjacent downstream portion of the run. Marked turtles were occasionally found there, mostly individuals that had originally been captured nearby but from within the study site. At the upstream edge of the study site, two forks of the run joined. Turtles were not found in either fork, but a sparse population of turtles existed above the point where the fork began, about 680 m upstream from the study site. No marked turtles were found in the area upstream from the fork on the two occasions it was searched.

Data for basking animals censused over a six-day period in Sept. 1983 were used to estimate population size using the weighted mean method (Begon, 1979).

Three *P. nelsoni* (one male, two females) on Paynes Prairie, Gainesville, Alachua County, Florida, were outfitted with radio transmitters (AVM) of approximately 27 mHz, attached by wire to two holes drilled through the rear marginals of the carapace. Relocations were taken at least daily for 24 days, from 27 June to 20 July 1986. The habitat of Paynes Prairie differs considerably from Rock Springs Run, and animals remained in an irregular shallow lake, created by a dam, until the water level fell. Two then moved to a canal bordering the lake. Movements of these animals were plotted on scale maps of the area.

Two methods were used to calculate home-range size of turtles in Rock Springs Run. In one, I used the maximum distance over water between relocations (Sexton, 1959) to estimate linear home-range size. In the second, I adapted Ford and Krumme's (1979) procedure to construct best-fit composite home ranges or population utilization distributions (PUDs) for different classes of animals.

All relocations of each turtle at Rock Springs Run were plotted on scale maps of the study site. The two most distant relocations, rounded up to the nearest 10 m, were used to estimate home range using Sexton's definition. Since individual turtles were often seen crossing the river and many individuals were relocated on both sides, I assumed that individuals used the full width of the river. These estimates of home-range size were regressed on plastron length, time between relocations, and the number of relocations per individual. Sex differences were tested using the Mann-Whitney U-test.

The distances between pairs of all combinations of relocations of each animal in a certain class (e.g., male *P. nelsoni*) were classified into discrete distance categories (the relocation distance function or RDF). I used the following categories: within 10 m, 10–20 m apart, 20–30 m apart, etc., to 990–1000 m apart (Fig. 1). GRG2 (L. S. Lasdon, A. D. Warren, and M. W. Ratner, GRG2 User's Guide, 1978, unpubl.), a FORTRAN program for solving constrained nonlinear optimization problems, was then used to reconstruct a composite home range for each class of animals. This procedure weights an individual's contribution to the RDF by the number of pairs of its relocations (e.g., two relocations give one pair, three relocations give three pairs, etc.).
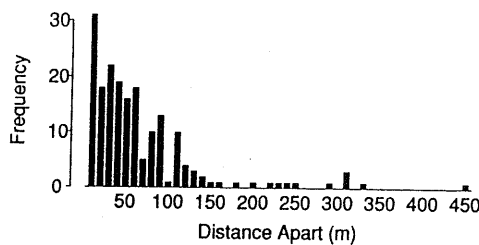
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Fig. 1. Frequency distribution of relocation distances (relocation distance function) of male *Pseudemys nelsoni*, including captures and all relocations except those from basking sites (n = 37), from Rock Springs Run, Apopka, Florida.
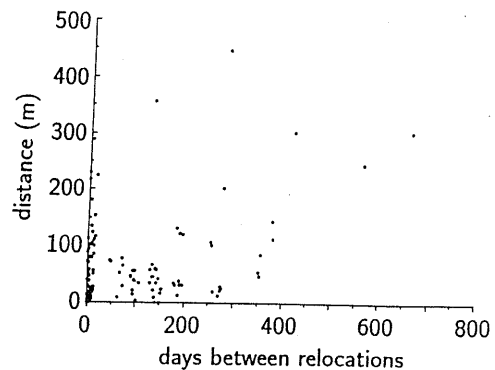

Fig. 2. Plot of the number of days and number of meters between relocations for male *Pseudemys nelsoni* from Rock Springs Run, Apopka, Florida. Basking site relocations are not included.

portion of relocations coming from each of the 100 "grids" of the composite home range and can be used to generate a hypothetical RDF. Solutions are constrained because the proportions (from each of the 100 grids) from the solution vector have to sum to one. The program returned a solution vector whose corresponding RDF was "closest" to the RDF from the data, quantified as the minimum sum of squared differences of corresponding values.

The program was usually unable to find an exact solution, but the RDFs from the data and from the solution had approximately the same distribution. In particular, the program was often unable to fit the tail end of the RDF (the few relocations separated by large distances) into the solution. Unlike variation attributed to the optimizer for solutions from two dimensional coordinates reported by Ford and Krumme (1979), solutions for these data were identical if the same starting point and initial proportions (used to "center" the solution in the grids) were entered. Solutions from other sets of initial proportions differed little or not at all, making several runs with the same data unnecessary.

One of the assumptions for using all relocations is that relocations are time independent. Figure 2 illustrates that the distance moved between locations was not a function of the time between them ($P > 0.25$). An additional assumption is that a composite home range can be interpreted. If sufficient relocations were available for each individual, the distribution of probabilities of recaptures throughout the home ranges should resemble each other and one based on many individuals but with few relocations per individual. Only for one turtle at Rock Springs Run, a male *P. nelsoni*, were sufficient relocations made to use Ford and Krumme's (1979) technique. The utilization distribution for this animal, based on 55 pairs of relocation distances, was similar to PUDs

composed of 42–45 pairs of relocation distances drawn randomly from other males.

When comparing classes of animals, a problem emerges; since solutions may not be unique, solutions cannot be directly compared. It is possible that several solutions fit the data about equally well. Ford and Krumme (1979) suggest a reliable and easily interpretable alternative. By plotting the minimum distance that contains a certain percent of the relocations (the cumulative probability of recapture), one can compare two or more solutions by the shapes of the curves. Further, a group can be subdivided and the solutions of each plotted to estimate the variance of the solutions. Thus, at any cumulative probability of recapture, one can obtain a mean minimum distance and its variance.

The cumulative probabilities of recapture and minimum distances containing these probabilities were calculated following Ford and Krumme (1979). Corridors, regions within the composite home range where the probability of recapture is zero, were not included in minimum distances. The probability of recapture at each 10-m grid of the home range was plotted on graph paper and the probabilities then connected with straight lines. At each change in slope or with the addition of a new peak, a minimum distance for that level was calculated by summing the distance below each of the peaks at that level. In addition, the area under the curve for each level was calculated with simple trigonometry. The total area under the curve was then divided into each of the successive cumulative areas to give a probability corresponding to the distance at that level (see Kramer, 1989, for an illustrated example).

TABLE 1. SAMPLE SIZES AND LINEAR HOME-RANGE STATISTICS FOR *Pseudemys nelsoni* AND *P. floridana* AT ROCK SPRINGS RUN, APOPKA, FLORIDA. Data-sets are based on captures and all relocations (with basking sites) or on captures and all relocations except basking site relocations (without basking sites).

Class	Number of individuals	Captures/relocations			Pairs of relocation distances	Home-range sizes (m)					
		Total	Mean	Range		Mean	Min.	Lower quart.	Median	Upper quart.	Max
Male *Pseudemys nelsoni*											
With basking sites	46	216	4.7	2, 19	634	132	10	43	90	140	730
Without basking sites	37	119	3.2	2, 11	186	111	10	40	90	130	450
Female *Pseudemys nelsoni*											
With basking sites	34	156	4.6	2, 17	492	207	10	43	90	213	990
Without basking sites	29	89	3.4	2, 12	122	139	10	40	80	115	890
Male and female *P. nelsoni* without basking sites	66	208	3.2	2, 12	308	124	10	40	80	125	890
Male and female *P. floridana* without basking sites	19	54	2.8	2, 6	57	298	10	80	260	460	840

Ford and Krumme's (1979) modified procedure, as outlined above, was applied to the following data sets: all male *P. nelsoni*, including and not including basking relocations; all female *P. nelsoni*, including and not including basking relocations; all female *P. nelsoni*, not including basking relocations nor relocations during the nesting season; four subgroups of male and three of female *P. nelsoni*, not including basking relocations; male and female *P. nelsoni* combined, not including basking relocations; and male and female *P. floridana* combined, not including basking relocations. There were insufficient relocations for *P. floridana* to subdivide this group further. Sample sizes for each data set are given in Table 1.

RESULTS

The total numbers of turtles tagged at Rock Springs Run were as follows: male *P. nelsoni*, 74; female *P. nelsoni*, 52; male *P. floridana*, 21; female *P. floridana*, 18. The mean plastron length of captured male *P. nelsoni* at Rock Springs Run was 224 mm ± 25 SD, and of female *P. nelsoni* 267 mm ± 32 SD. It is likely that the smaller females marked were not mature (Jackson, 1988). The radio-tracked male at Paynes Prairie measured 231 mm, the two females 295 mm and 306 mm.

The estimate of population size of adult (and subadult female) *Pseudemys* turtles in the Rock Springs Run study site was 302 ± 34 SE. Using the proportion of *P. nelsoni* to *P. floridana* captured to estimate the proportion in the study site, there were about 231 *P. nelsoni* and 71 *P. floridana*.

Estimates of linear home-range size for *P. nel-soni* based on Sexton's definition were highly variable, ranging from 10–990 m (Table 1). Mean home-range length is presented for comparison with other studies. However, since the distributions of home-range lengths are non-normal, values delimiting quartiles of the distributions are also provided. These estimates were not a function of the number of relocations per individual ($P > 0.25$) nor the number of days between relocations ($P > 0.25$). Similarly, I found no sex differences or effects of body size ($P > 0.25$). Most relocated animals moved little among relocations (Fig. 1). Even after several years, I found few marked turtles outside the study site. Although no relocated *P. floridana* had moved more than 840 m, mean home-range estimates were larger than for *P. nelsoni*. In addition, both the mean number of relocations per individual and the percent of marked animals that were relocated were smaller (Table 1).

All relocations of male and female *P. nelsoni*, including basking site relocations, were used to construct a PUD for each sex. The distributions were similar, both exhibiting a large peak near one end of the home range (Fig. 3 shows results for male *P. nelsoni*). The peak is likely a result of basking relocations, giving rise to a large proportion of relocations within 10 m of a previous one. After removing the basking relocations from the data, the resulting PUDs lost this single large peak (see Fig. 3). The data were reanalyzed without basking site relocations to estimate size and use of the aquatic portion of the home range.

The distances encompassed by the PUDs for male or female *P. nelsoni* (Table 1) are generally smaller than the mean (but not median) home-

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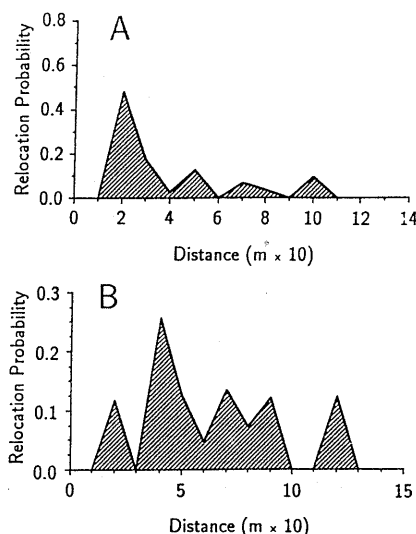on of the

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Fig. 3. (A) Population utilization distributions of male *Pseudemys nelsoni* from Rock Springs Run, Apopka, Florida, from all captures and relocations. The left-right orientation is arbitrary. (B) Population utilization distributions, from all captures and relocations except basking sites, of male *P. nelsoni* from Rock Springs Run, Apopka, Florida.
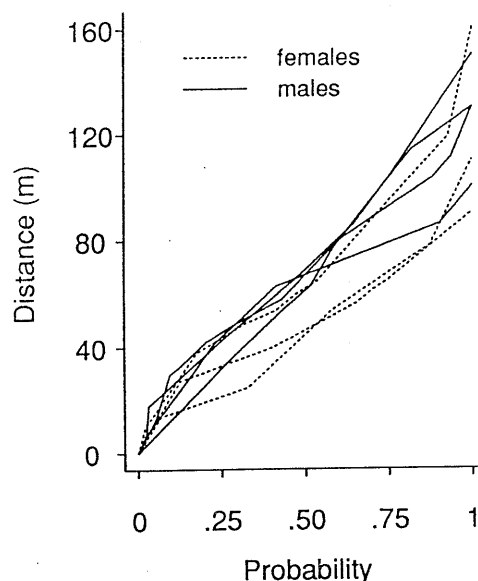
Fig. 4. Minimum distance vs cumulative probability of recapture for four subgroups of male and three of female *Pseudemys nelsoni*, from all captures and relocations except basking sites.

range size estimated using Sexton's (1959) definition, consistent with Anderson's (1982) finding that Ford and Krumme's (1979) technique underestimates home-range size. Since female *P. nelsoni* may leave their regular home ranges during the nesting season, I removed summer relocations (Jackson, 1988) of females and recalculated their PUD. The resulting home-range estimate was actually slightly larger than the estimate with summer relocations. Thus, I concluded that nesting movements were not affecting the home-range size estimates. To test for sex differences, males and females were first subdivided into groups with 39–55 pairs of relocation distances/group. A composite home range was then constructed for each of these data sets and the results graphed as cumulative probability of recapture vs minimum distance (Fig. 4). There were no significant differences between males and females, whether using 0.95 or 0.50 probability (the latter suggested by Anderson, 1982). Therefore, data for both sexes were combined and a PUD and probability vs minimum distance for all *P. nelsoni* calculated (Fig. 5). Since data for *P. floridana* were insufficient for subgrouping, calculations were made for both sexes combined (Fig. 6).

It is clear that, by using either a linear measure or Krumme and Ford's technique, the home

range of *P. nelsoni* is smaller than that of *P. floridana*. This is consistent with a higher relocation rate for *P. nelsoni* since *P. floridana* individuals, with a larger home range, would be more likely to include areas outside the study
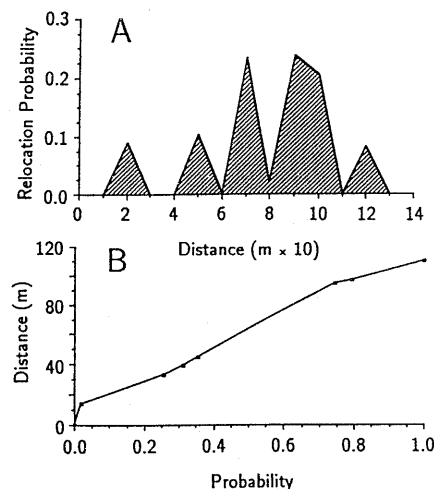
Fig. 5. Population utilization distribution (A) and minimum distance vs probability plots (B), from all captures and relocations except basking sites, of male and female *Pseudemys nelsoni* from Rock Springs Run, Apopka, Florida.
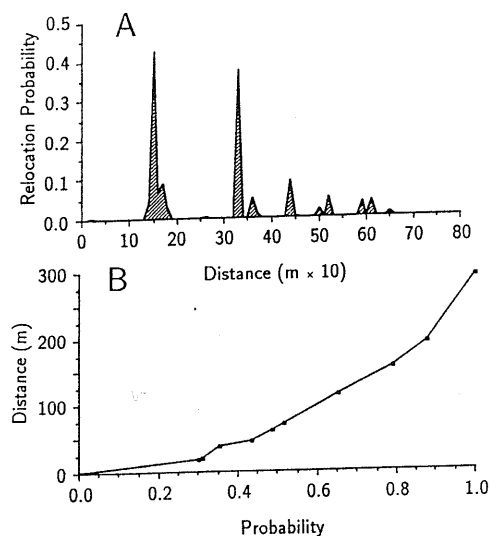
Fig. 6. Population utilization distribution (A) and minimum distance vs probability plot (B), without basking site relocations, of male and female *Pseudemys floridana* from Rock Springs Run, Apopka, Florida.

site. Using Ford and Krumme's technique, the composite home range for *P. nelsoni* in Rock Springs Run appears to comprise about 120 m of river length including a short "corridor" in which the animal is unlikely to be relocated. In comparison, the composite home range of *P. floridana* is about 650 m with many corridors of various lengths.

Movements of radio-tracked animals on Paynes Prairie were erratic. Animals appeared to spend a few days in a small area, then move to another area and stay there for a few days. A map of the movements of these animals is given in Kramer (1989). Although all three animals moved about greater distances than those in Rock Springs Run, they all remained in the portion of the lake or neighboring canal near the initial point of capture. During one week, all relocations of one of the females were within 50 m of each other. On 13 July, the male burrowed into the mud substrate (to a depth of about 50 cm) and remained there until he was dug up to remove the transmitter on 16 July. Lake levels were falling rapidly at this time, and two days later both females moved into a canal bordering the lake and a dike. I terminated data collection on 20 July because the turtles were prevented from moving freely about the study area due to both low water levels and potential predation from the numerous alligators that congregated in regions of the lake still holding water. Using the minimum convex polygon

method (Southwood, 1966), the total (T) and aquatic (A) home ranges (where any land area is subtracted from T; see Schubauer et al., 1990), in hectares, of these individuals were as follows: 16.2 T, 13.3 A and 17.5 T, 14.1 A for the two females, and 31.0 T, 20.6 A for the male. By comparison, the largest home range for an individual at Rock Springs Run is less than 3 ha, assuming the average width of the river to be 30 m.

DISCUSSION

All known techniques for assessing home-range size have problems (Schubauer et al., 1990). The two techniques used to relocate turtles described in this study were not used at the same study site and thus cannot be directly compared. Although capturing underwater by hand/resighting may be less problematic than mark/recapture by trapping, most mark/recapture techniques suffer from the small number of relocations per individual. This will, in general, bias results so that measures of central tendency of the distribution of individual home-range sizes using mark/recapture underestimate a "true" average home-range size. This is clearly shown by Schubauer et al. (1990) for *Trachemys scripta* in a lake. Further, it is not clear how to compensate for this bias. There is no reason, however, that results from mark/recapture studies cannot be compared, as long as the methodologies and numbers of relocations per individual are similar. In general, results reported here for *P. nelsoni* are similar to those for *T. scripta* in Schubauer et al. (1990) for data collected using similar techniques.

A comparison of the PUDs of the two species examined in this study is instructive. Not only do areas with positive probabilities of recapture appear to be more patchily distributed throughout the composite home range of *P. floridana*, the cumulative probability curve has a distinctly concave shape (Fig. 6). This indicates that considerable variation of the probabilities exists among areas with positive probabilities of recapture. The much flatter curve for the composite home range of *P. nelsoni* (Fig. 5) indicates more even use of the home range. This suggests that *P. floridana* has different requirements from *P. nelsoni*, and thereby requires a larger home range to ensure that individuals have adequate resources.

Although less patchy than that for *P. floridana*, the PUD for *P. nelsoni* suggests that individuals use their home range unevenly, possibly resulting from a heterogeneous resource distribution. I speculate that the patchy distri-

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bution of aquatic resting sites (see below) is the most likely heterogeneously distributed resource to explain the distribution of relocations (see also Florence and Murphy, 1976; for a similar conclusion about small mammals, see Don and Rennolls, 1983).

Although microhabitat variables were not quantified at this study site, I offer the following generalizations, based on subjective impressions. Turtles were most often captured and relocated in or near areas that provided support for animals resting near the surface with their heads above water, especially if there was overhanging vegetation from the bank. These resting sites consisted of emergent vegetation (e.g., *Nuphar* sp., *Pontederia* sp., or *Typha* sp.) and supports derived from shoreline vegetation, such as submerged trees, branches, or piles of branches. This is probably why one area of the study site was well frequented, since resting sites, overhanging vegetation, and basking sites were present throughout most of a 200 m distance. Even there, turtles were unlikely to be found in gaps in the supporting or overhanging vegetation. There were few relocations from the middle of the run, shallow (< about 30 cm) waters adjacent to the bank, strong currents, or waters deeper than about 2 m, although turtles were seen in all these situations on occasion.

Results from constructing the various PUDs of male and female *P. nelsoni* and from other studies (e.g., Auth, 1975) suggest that home ranges of semiaquatic emydid turtles typically include a basking site. If true, basking sites may be a limiting resource at Rock Springs Run, forcing at least some animals to extend or construct their home range so as to include a basking site. Turtles were rarely found in long stretches of the river devoid of basking sites. Lack of basking sites and other resources typically located near the water-land boundary may explain why home ranges were so much larger on Paynes Prairie, since it is likely that in the lake a much smaller percentage of the home-range area contained resources used by turtles.

There is an apparent lack of association between time and distance between relocations. One might suspect that, in general, distance between relocations should increase with time, the association weakening until, given enough time, relocations become independent of each other. There are two reasons this relationship may not have been detected for turtles in Rock Springs Run. First, the small home ranges of *P. nelsoni* there could be traversed by an individual turtle in well under an hour. Since very few relocations were made less than one day apart, the time to independence between relocations may

have been surpassed by even the closest pair of relocations in time. Second, the effect of diurnal cycles can complicate the relationship between time and the distance between relocations (Swihart and Slade, 1985) such that independence occurs only in a "window" of the 24-h cycle. Individuals may show spatial and temporal fidelity to certain areas within their home range. Relocations 24 h apart would probably not be independent in this case. However, the radio-tracked turtles at Paynes Prairie, relocated once in the morning and again in the afternoon, weather permitting, exhibited no evidence that a diurnal movement pattern existed. Individuals at Rock Springs Run usually basked on the same log or group of logs, although perhaps not daily. Since most basking sites were in full sun only part of the day, basking relocations of individual animals should be fairly predictable. Auth (1975) documents this for *T. scripta*.

Home-range research done by others on related species have yielded widely disparate estimates, apparently due to factors other than methodology, e.g., habitat. For example, Pearse (1923) found that most of the painted turtles (*Chrysemys picta*) he marked in a bay of a lake moved less than 100 m during the course of his study whereas those studied by MacCulloch and Secoy (1983) in a river moved an average of more than 2 km, and one male traveled 6.5 km in a day. The ability of *P. floridana* to travel distances exceeding their home range was noted earlier by Marchand (1945), who stated that his estimate of home range in a river was less than 300 yds (277 m). His estimate is less than the 650 m of this study using Ford and Krumme's (1979) technique but close to the mean using Sexton's (1959) "maximum distance over water" method. Estimates of the home range and movements of *T. scripta* also differ considerably among studies (reviewed by Bury, 1979, and Schubauer et al., 1990).

Home-range size may reflect resource distribution, with smaller home ranges in areas where all required resources are abundant. Unfortunately, other than proximity to basking sites and food, our understanding of what resources are needed by these species is limited. Overlying minimal physical requirements are constraints due to these species' intra- and interspecific social organizations. Again, knowledge of social behavior of these species is scanty. Relatively fixed home-range size in different habitats might indicate that the social system is the predominant determinant of home-range size whereas variable home-range size might indicate a more flexible social structure, allowing resource distribution to dominate. The causes of individual

variation in home-range size within the same habitat may be more difficult to understand. Much of it may be due to noise in measuring individual home-range size or, on the part of the animal, to real or perceived intrasite differences. However, home-range size differences may also be due to strategy, size, sex, experience, ability, and the like. In this study, results suggest that both intra- and intersite variation exists. Why this occurs awaits the results of future studies.

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