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Temporal and Spatial Movement Patterns of Sliders and Other Turtles

Abstract

Movement by turtles can be considered spatially in terms of whether it is intrapopulation or extrapopulation. Intrapopulation movements are primarily for purposes related to feeding, reproducing, basking, and hiding. Extrapopulation movements are primarily for purposes of migrating between seasonally variable habitats, abandoning unsuitable habitats, nesting by females, and mate searching by males. The daily and seasonal timing of movement varies among species in response to environmental, physiological, and demographic conditions. Data on slider turtles (*Trachemys scripta*) and other freshwater species in South Carolina indicate that movement by many individual turtles is highly directional and consistent among years, although environmental variability influences timing and direction. Suggestions for future research are given, based on findings with slider turtles and previous reports in the literature.

Introduction

Movements within and among animal populations are critical to a variety of life history and ecological processes. Identifying the temporal and spatial patterns of movement by individuals of a population is prerequisite to understanding the ecological and evolutionary reasons for dispersal, migration, or intrahabitat movements by individuals of a species. The purpose of this chapter is to consider movement phenomena of turtles in the context of the slider turtle (*Trachemys scripta*) and other species of freshwater turtles collected over a 20-year period on the Savannah River Plant (SRP) in South Carolina (Gibbons, 1987). Although the material presented is mostly descriptive, the information should answer certain questions about movement phenomena in turtle populations, serve as the foundation for future questions, and lead to experimental approaches to answer those questions.

Table 16.1. General factors potentially influencing movements of turtles in a population

Environmental	Demographic
Daily temperature patterns	Population density
Seasonal temperature patterns	Sex ratio
Weather events	Age structure
Habitat type and condition	Size structure
Maturity and physiological state	
Sex	
Body size	
Recent experience	

Movement by individuals in a turtle population can be categorized spatially in terms of whether it is intrapopulation or extrapopulation and temporally in terms of whether it occurs on a daily, seasonal, or sporadic basis. Movement by an individual may be in response to or as a consequence of local environmental situations and events; demographic features that characterize the population, such as sex ratio and size and age structure; or the reproductive or other physiological conditions of individuals in the populations (Table 16.1). A discussion of what constitutes a freshwater turtle population is given in Chapter 1, and it is apparent that no definition of a turtle population is totally satisfactory for all circumstances and considerations. For the lentic-habitat species occurring on the SRP, a population generally is considered to be the individuals of a species inhabiting an identifiable aquatic habitat. Therefore, for the purposes of discussion in this chapter, terrestrial departure from a circumscribed aquatic habitat or any long-distance movement of more than 0.5 km is defined as extrapopulation. This definition will in some instances encompass terrestrial movements (such as some nesting excursions) in which the individual actually returns to the same aquatic habitat.

A premise in this chapter is that the movements of animals are not random but are directed in terms of leaving or reaching a particular location or are driven by some other motive. Thus, a painted turtle may move directly and unerringly toward a favorite basking log or to a particular feeding site to which it has been on other occasions. Or a male slider turtle may wander away from an aquatic habitat in what is seemingly a trip without a plan, though he has a primary motive: to find a receptive female for mating. His movements, therefore, are those that have the highest probability of achieving this goal. Thus, movement by turtles is assumed to have some probability of benefit to the individual and is balanced by negative feedback of various sorts. Some obvious potential costs of movement by an individual turtle are an increased risk of predation and possibly exposure to desiccation or thermal extremes that may confront overland travelers. In addition, all movement requires an expenditure of energy and therefore an energy cost.

One approach to examining movement patterns by turtles is to quantify distances and directions moved and time spent moving, within the framework of spatial categories (intrapopulation and extrapopulation), temporal categories (daily, seasonal, and sporadic), and particular purposes (Table 16.2). If these patterns can then be coupled with an assessment of risks (costs) and benefits and a consideration of how natural selection operates on movement patterns, we will be closer to understanding the significance of why turtles move and to predicting when and where their movement is most likely to happen. Our objective in this chapter is to quantify the movement of freshwater turtles in as many of the defined categories as possible and to discuss the ecological and evolutionary significance of the findings.

Intrapopulation movements are made by turtles for

Table 16.2. Categories of movement by individual turtles and factors that must be assessed when considering movement phenomena

Category	Purpose	Primary benefits potentially gained by moving
Intrapopulation (short-range)	Feeding	Growth; lipid storage
	Basking	Increased mobility due to body temperature increase; reduction of external parasites; enhanced digestion
	Courtship and mating (adults only) Hiding, dormancy	Reproductive success Escape from predators or environmental extremes
Extrapopulation (long-range)	Seasonal	Growth; lipid storage
	Seeking food resources	Direct increase in fitness
	Nesting (adult females)	Direct increase in fitness
	Mate seeking (adult males)	Survival
	Migration (hibernation; estivation)	Initiation of growth
Travel from nest by juveniles	Survival	
Departure from unsuitable habitat	Survival	

Note: Movement for each purpose needs to be placed in the contexts of daily and seasonal timing.

four obvious purposes: (1) feeding, (2) reproduction (mate seeking, courtship, and nesting), (3) basking, and (4) seeking favorable sites in which to hide or remain dormant for extended periods (Table 16.2). Additional reasons also exist, but these are the four most apparent ones.

Extrapopulational movement, as defined above, can be categorized either as seasonal and generally predictable activity or as abandonment of a habitat that has become unsuitable. Seasonal movements of freshwater turtles can be attributed to (1) overland movement by hatchlings from nest to aquatic habitat, (2) searching for resource features of a habitat that vary seasonally in their availability or importance to individuals in the population, (3) departure to or return from overwintering sites, (4) searching by adult males for receptive females during circumscribed mating periods, and (5) nesting by females. A consequence of long-range movement by turtles is increased genetic exchange among populations (Scribner et al., 1986; also see Chapter 6), but this cannot be considered as a reason for movement without more-elaborate theoretical arguments than are warranted in this presentation.

Risks and Benefits of Movement

Movement patterns among turtle species can theoretically be quantified in terms of probable risks (costs) and benefits, assuming that taking risks associated with some aquatic or overland movement has a probability of positive returns that are greater than the probability of negative consequences. For example, the traveling by some freshwater turtles, at some risk of predation, of long, seemingly unnecessary distances from water to lay eggs is presumably warranted in terms of natural selection, because proper choice of a nesting site results in a higher fitness probability. Such risks can be carried to extreme, of course, and a point can be reached at which the probable risk of predation outweighs the probability of a fitness gain from finding a proper nest site.

This type of risk-benefit relationship is presumably balanced by natural selection within a population, with some individuals overextending themselves in the risk category while others err on the conservative side of risk taking and do not fare as well with the potential benefits. Naturally, local environmental circumstances can shift the balance in one direction or another. For example, the female turtles on an island with no terrestrial predators should be less constrained in nest-seeking behavior, and the highest fitness probabilities would lie with individuals that would be extreme risk takers on the mainland.

The primary risks in various categories of movement (Table 16.2) are those that can result in death of the individual through increased exposure to predators, thermal extremes, and desiccation. Among freshwater species the latter two risks would be mainly restricted to ter-

restrial activities. Each of these risks is presumably dependent on body size within a species and should be assessed in these terms. Also, sex and stage of maturity should be considered significant factors in the level of risk because behaviors may differ among individuals in the different categories.

In addition to the more dramatic risks of predation and environmental extremes are the low-level risks associated with expenditure of energy. Any movement requires energy. Thus, by moving from one location to another, the organism risks using more energy than is warranted by the ultimate benefits.

Quantitative data for comparing risk and benefit probabilities for various categories of movement by turtles are not available, to our knowledge, from any study. In fact, only limited quantitative information is available from this study and a few other studies of the temporal and spatial aspects of movement in the intrapopulational and extrapopulational categories that have been identified (Tables 16.1 and 16.2). Turtle biologists should (1) further refine the movement categories in which risks and fitness benefits can be quantified, (2) continue to determine the extent of the movement within and among populations, and (3) strive for the ultimate goal of assessing the significance of the movement patterns in terms of relative risks and benefits.

Spatial Activity

The long-term SRP studies with large numbers of captures in a variety of habitats in a region provide an opportunity to quantify phenomena that occur on an infrequent as well as a regular basis. Although some emphasis has been placed on movement patterns of turtles within habitats on the SRP (see Chapter 18), extrapopulational movement has received the greatest attention. The exchange of individual turtles among aquatically disconnected habitats that are distant from one another (see Chapter 2) has been repeatedly confirmed through the recapture of individuals that have moved.

Intrapopulational (Short-range) Movement

Many ecologists, including turtle biologists, have focused on establishing some form of home-range quantification for their study species. The approaches, biases, qualifying considerations, and even the definitions associated with home-range determinations seem endless and are beyond the scope of this book. A discussion of some approaches for considering home range is given in Chapter 18.

Home-range calculations and point-to-point movements reported by turtle biologists suggest that some species use relatively large amounts of habitat, whereas others are much more restricted in their movement patterns (e.g., Ernst, 1968a,b; Hammer, 1969; Mahmoud, 1969;

Ernst, 1970c; Moll and Legler, 1971; Bury, 1972; Brown, 1974). In general, larger species move longer distances than smaller species do, and adults are more likely to move farther than juveniles. A caution must be observed not to overinterpret findings as characterizing a species, because of the inherent biases associated with the particular time and place that a study was done, especially if the study was conducted over a short period that did not incorporate a variety of annually variable environmental situations.

Although intrahabitat movement patterns are a significant area for research, our studies on the slider turtle and other freshwater species in South Carolina can contribute little to the quantification of short-range movements within populations because we did not focus on intrapopulation movement and have few meaningful measurements. However, such research will be necessary to provide a foundation for developing quantitative models of movement patterns and intrapopulation risk-benefit assessments (Tables 16.1 and 16.2). The questions to be asked can be stated as follows:

1. What is the total amount of intrapopulation movement, and what is the level of variability in movement among individuals and among populations of a species?
2. What are the timing and the amount of movement that is directed toward achieving particular goals?
3. How are the risk probabilities and energy costs of intrapopulation movement balanced against the potential benefits of particular movement patterns?

Acquiring answers to these questions can lead to understanding why turtles expend energy and risk predation in intrapopulation movement and how the extent of such movements is controlled by natural selection. Of course, one potential answer for some, perhaps most, situations is that the risks associated with intrapopulation movement are trivial and that the emphasis should be placed on the benefits gained by such movements. Nonetheless, the question of why turtles move about within a population is a valid inquiry, and the questions listed above must be answered if a level of predictability of the phenomenon is to be achieved.

Extrapopulation (Long-range) Movement

Long-range movements associated with nesting by females, mate-seeking behavior by males, or other seasonal behaviors are predictable activities that occur annually. Thus, observations or experiments can potentially be planned to quantify these in a population. Information on forced migration from an unsuitable habitat is more difficult to acquire because of its unpredictability. Although a

population may respond to adverse conditions, the opportunity for the investigator to observe the phenomenon may not arise. Nonetheless, each of these categories of long-range movement deserves attention in a consideration of turtle populations and has been addressed to some degree by the studies on the SRP. Because of the large data base and the high variation in timing, distance, and direction of movement among individuals, it is most expedient to address extrapopulation movement by examining selected segments of the data.

RECAPTURES IN OTHER LOCATIONS

Records of individuals that were originally captured at one site and subsequently recaptured at another confirm that interpopulation exchange has occurred. Another approach, use of the terrestrial drift fence and pitfall traps, can provide circumstantial evidence of extrapopulation movement by individuals, assuming that those captured at the fence have intentionally departed from the aquatic habitat and are thus leaving the population. The limitation of the technique is that the ultimate destination of an individual is not known, so the potential distance traveled is not determined. However, the timing and other features of extrapopulation movement can be established for turtle species with this technique.

Besides mark-recapture and the drift fence technique, an unusual situation exists on the SRP for documenting the propensity of turtles to move extrapopulationally. A population of *T. scripta* and a few individuals of other species inhabited a radioactively contaminated area (A-Area Seepage Basins) for many years (Gibbons and Congdon, 1986). Until 1983 the basin area was unfenced, and turtles had free overland access to other bodies of water in the Lost Lake System. Because the A-Area Seepage Basins were the only ones of this type in the vicinity, the next closest seepage basin being 8 km away from Lost Lake, any turtle captured in the Lost Lake System and detected as radioactive was assumed to have been an inhabitant of the A-Area Seepage Basins at one time. A portion of the long-range movement data (Fig. 16.1) is based on such captures.

Slider turtles were by far the most commonly recaptured species on the SRP at sites different from the one of original capture. Of the 4,768 individuals from Ellenton Bay, Par Pond, and the Lost Lake System that had been marked during these studies, 244 were verified to have made extrapopulation moves to other habitats, ranging from 0.2 to 9 km away from their original capture sites. The minimum distances traveled, based on the shortest straight-line measurements between habitats, are consistently higher for males than for females (Fig. 16.1), even when the male-biased sex ratios in this species (see Chapter 14) are taken into account. Few recaptures of juveniles have been made at other sites, suggesting that successful

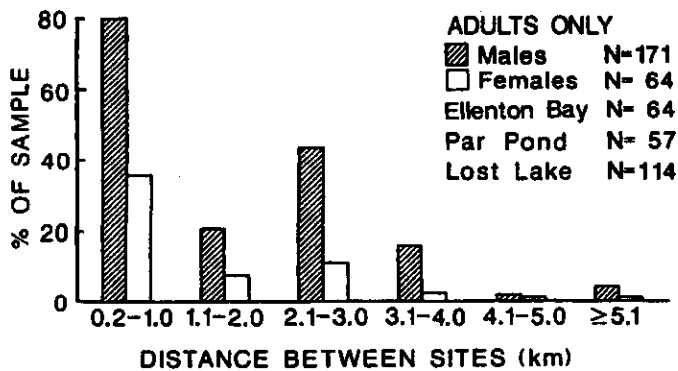


FIGURE 16.1. Distances of long-range movement (more than 200 m) by adult *T. scripta* on the SRP, based on recapture of individuals in habitats other than the one of original capture. Ellenton Bay and Lost Lake exchanges were primarily between habitats not connected by waterways, so the majority of travel was overland. All measurements are given as straight-line, minimum distances. Most of the exchanges in Par Pond could have been achieved by aquatic travel for longer distances along shorelines. Radioactive turtles captured in Lost Lake sites were assumed to have been in the A-Area Seepage Basins at some earlier time (see text).

extrapopulational movements are more common for adults (Fig. 16.2).

Evidence that movements by turtles from one habitat to another are not dead-end trips is given by the ultimate recapture of individuals in their habitat of original capture following intermediate recapture at another site. Individual *T. scripta* that traveled extrapopulationally and then returned to the site of original capture included individuals from Par Pond ($N = 3$), Ellenton Bay ($N = 17$), and the Lost Lake System ($N = 6$). Whether such movements represent typical annual migration patterns between habitats by certain individuals or whether they are responses of individuals to alternating unsuitable habitat situations is unknown at this time. Determination of the regularity of such occurrences and the proportion of the population of a species that alternates between habitats would be extremely useful in the interpretation of movement patterns.

In addition to revealing long-distance movement, the turtles from the A-Area Seepage Basins provided a second measure of comparative vagility of the sexes. The body burden of radioactivity of an individual inhabiting the basins indicates the period of time it has been there. An individual that had departed the habitat would not continue to have an uptake of radioisotopes, and the primary gamma-emitting isotopes (cesium-137, strontium-90) have a finite biological half-time of only a few months (Scott et al., 1986). Therefore, an individual that had left the basin and returned or that had entered from another habitat would have a lower body burden than a longer-term resident. Based on this idea, we measured the level of

radioactivity of turtles of both sexes that were captured in the basins (Fig. 16.3). The conclusion is that females are more sedentary, as is indicated by their significantly higher body burdens of radioactive cesium and strontium. This is converse evidence that males are more likely to move among habitats, thus spending less time at any specific location.

DRIFT FENCES WITH PITFALL TRAPS

A total of 8,412 captures and recaptures of six common species of turtles was made at drift fences in three separate locations (Ellenton Bay, Risher Pond, and Rainbow Bay) on the SRP. Additional captures were made at several other study sites where sampling was for less than two years or where turtles were a minor part of the herpetofauna, but the three sites named above provided the primary data on extrapopulational movement based on drift fence data.

During certain years Ellenton Bay provided the opportunity to examine whether particular size classes were more likely to move extrapopulationally when overland movement was optional rather than forced by drying of the aquatic habitat. Although individuals smaller than 10 cm in plastron length constituted an appreciable portion of the population, few of them left Ellenton Bay during the four-year period (1975-78) during which the bay was encircled by the drift fence and water levels remained high. Males began leaving the aquatic habitat upon reaching the size of sexual maturity (≈ 100 mm plastron length). A high proportion of individuals in each size category that exited from the bay did not return within a year. Immature females in the size category of 12 to 15 cm began departing from the bay with increasing frequency, relative to those in smaller size classes. However, the greatest numbers of exiting females were adults (Fig. 16.4). One conclusion from these data and from Figure 16.2 is that larger turtles are more likely to leave the aquatic habitat than smaller individuals are. Another is that size per se, independent of reproductive condition, is an important component of extrapopulational movement, because immature females 12 to 15 cm in length moved frequently. Nonetheless, the advent of maturity in both sexes is the strongest correlate with a propensity to travel. A general comparison among species indicates that adults of each of the six species of turtles inhabiting Ellenton Bay are more likely to make overland excursions than are juveniles.

These data are circumstantial evidence of extrapopulational mobility by individual *T. scripta*, although the final destination is known for few. The terrestrial behavior of *Kinosternon subrubrum* indicates that this semiaquatic species makes excursions away from the aquatic habitat for a purpose (hibernation) besides travel to other aquatic sites, although a few individuals have been known to relo-

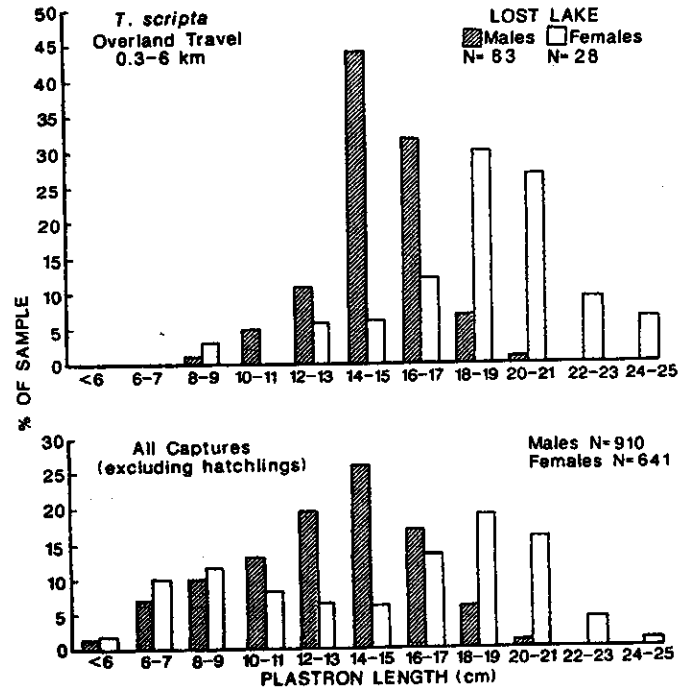
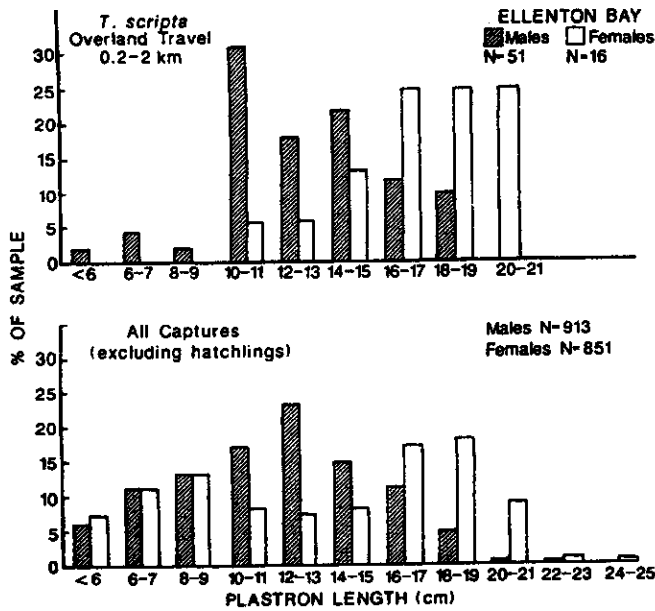
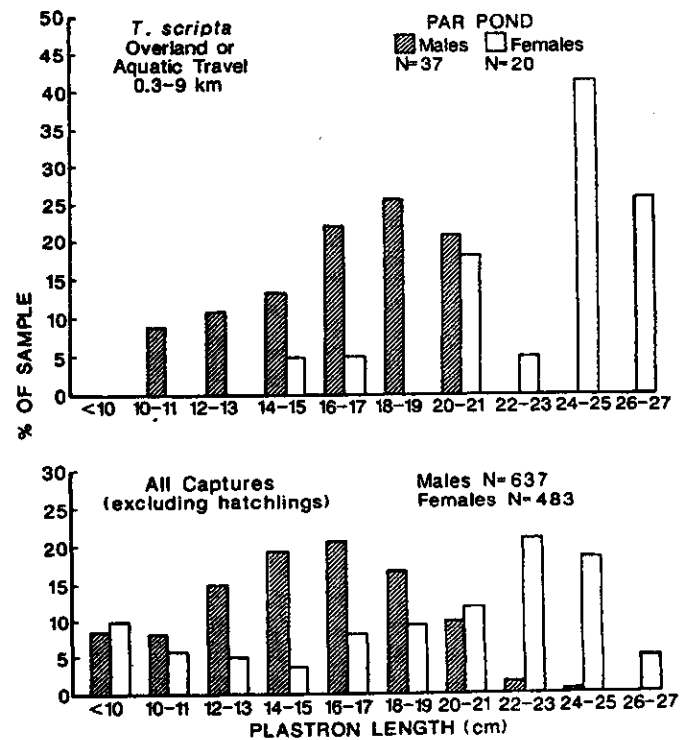


FIGURE 16.2 (ABOVE AND RIGHT). Sizes of *T. scripta* exhibiting travel between aquatic habitats, based on recapture in a habitat other than the one of original capture (see Fig. 16.1). Plastron lengths are the minimum sizes at which individuals were known to have traveled. Bottom graphs for each habitat represent total numbers of individuals captured in each size-sex category in the same study population, based on sizes of individuals at last capture. The overland travel at Ellenton Bay includes drought years in which most individuals left (Gibbons et al., 1983).



cate in other habitats (Gibbons, 1986). Little evidence is available to indicate the extent to which other species will burrow at the soil and litter surface upon leaving an aquatic area, but we are aware of a few instances of such behavior in *T. scripta* and *Deirochelys reticularia*. Therefore, the evidence that major segments of a population depart the aquatic area must be viewed cautiously in terms of the purpose or destination. Movement identified by drift fences is extrapopulational, as defined earlier, but movement to another aquatic site is not a requisite feature.

Based on the drift fence data and the evidence from recaptures of individuals at sites other than their original one, it is apparent that overland movement occurs among sliders and other turtles generally considered to be aquatic. A variety of explanations can be given for terrestrial movement by aquatic species, assuming that overland travel is a risky business for a turtle and must have some potential benefit to the individual that outweighs the risks. One explanation relates to sex and reproductive purpose.

NESTING FEMALES

Movements to nesting sites may be classed as intra-populational in that the females, in many instances where

data are available, generally return to the aquatic habitat from which they came, although the return trip may not be immediate. It should be noted that a major segment of the Ellenton Bay adult females leaving the aquatic habitat did not return the same year (Fig. 16.4). Many of these departures were known to be nesting excursions, because

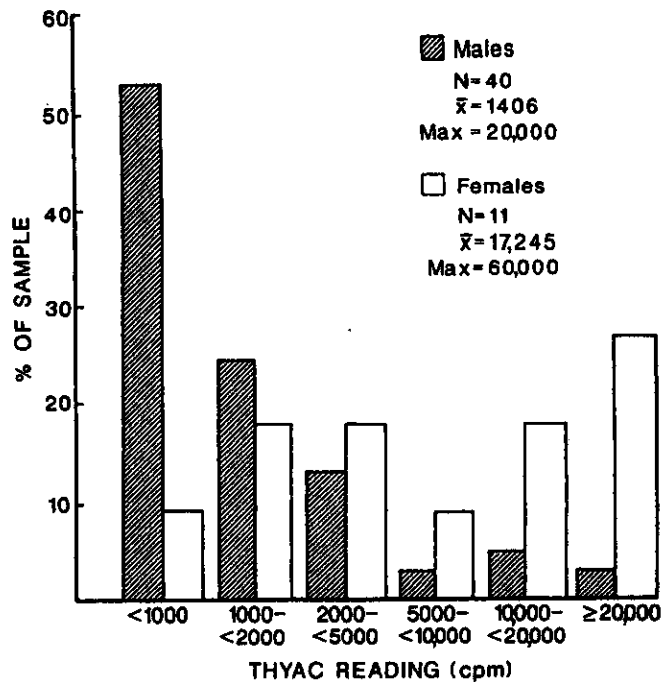


FIGURE 16.3. Levels of radioactivity, primarily from cesium-137 and strontium-90, as determined by Thyac readings of the carapace of 51 *T. scripta* inhabiting the A-Area Seepage Basins on the SRP. All individuals from the basins had readings above background—normally less than 100 counts per minute (CPM)—for the region.

the females were carrying fully shelled eggs. Because of the freshwater turtle biologist's bent for thinking of the population as being centered around a particular aquatic habitat where most of the individuals stay most of the time, we have arbitrarily assigned such movements as a special case in the extrapopulation category.

Many species of turtles are known to make long-distance movements to find suitable nesting sites. Cagle (1950) observed slider turtles (*T. scripta*) in Louisiana traveling more than 1.6 km overland to nest. Moll and Legler (1971) observed nesting females of this species in Panama up to 400 m from the nearest water. Plummer and Shirer (1975) reported female softshell turtles (*Trionyx muticus*) moving 2 to 6 km down a river to nest. Female snapping turtles (*Chelydra serpentina*) in Canada traveled more than 5 km to a particular nesting site, and the same general area was chosen by the same females each year (Obbard and Brooks, 1980). For their small size, even nesting *K. subrubrum* travel relatively long distances, based on their capture at the Ellenton Bay drift fence more than 50 m from the water's edge. Burger and Montevecchi (1975) found that diamondback terrapins (*Malaclemys terrapin*) selected nest sites in high dune areas approximately 150 m from the closest water. Truly marine species move the longest distances. The records for marine turtles that may travel hundreds of kilometers

from feeding areas to nesting beaches are widely recognized (Carr, 1965).

The most detailed report on travel by nesting freshwater turtles has been by Congdon et al. (1983b) for the Blanding's turtle (*Emydoidea blandingii*). Studies on the E. S. George Reserve in southern Michigan revealed that a few females with eggs travel more than 1 km overland, presumably in search of a favorable nesting site. Fidelity to general nesting areas was observed from year to year, but females did not necessarily return to the same area each nesting season. However, particular care about where their eggs were laid was displayed by females in each instance. Females of both *E. blandingii* and *C. serpentina* (Congdon et al., 1987) characteristically returned to their original aquatic habitats after nesting.

Identifying nesting activity by terrestrial species as extrapopulation is more difficult because of the uncertainty in many cases of what constitutes the normal activity area of a population. Species in the genus *Gopherus* are apparently able in most instances to find suitable nesting sites without making unusually long treks. Although gopher tortoises (*G. polyphemus*) have been reported to nest several meters away from their burrows (Iverson, 1980; Landers et al., 1980), Landers et al. (1980) reported that 85% of 110 nesting sites in Georgia were in the vicinity of burrows, some being within the burrow mound. The Bolson tortoise (*G. flavomarginatus*) may also lay its eggs in or near its burrow (Morafka, 1982). Berlandier's tortoise (*G. berlandieri*) does not build a conventional burrow but has not been reported to travel long distances for nesting (Auffenberg and Weaver, 1969; Rose and Judd, 1982). Ernst and Barbour (1972) stated that eggs of the desert tortoise (*G. agassizii*) are "occasionally laid in the mouths of burrows." Most desert tortoises apparently nest inside burrows (F. B. Turner and Kristin H. Berry, pers. com.). Long-distance movements by females for nesting could occur, because the burrows used by an individual in a colony may be far apart, but we would not construe this to be extrapopulation.

The studies on SRP turtles add little to an understanding of the factors influencing the distance traveled by nesting females. However, the information from the drift fence and pitfall traps at Ellenton Bay provides evidence of the level of directional fidelity of nesting females in terms of their departure from the aquatic habitat. It should be noted that few females were followed to their chosen nesting sites, and the drift fence data indicate only the general direction of movement several meters from the water's edge. However, the variability among individuals of a population in their choice of direction for nesting (Fig. 16.5) was much greater than the consistency shown by individuals in their choice of direction in different years (Tables 16.3 and 16.4). Thus, the directions taken by nesting females ($N = 420$) of six species at Ellenton Bay were not equally distributed around the perimeter ($p <$

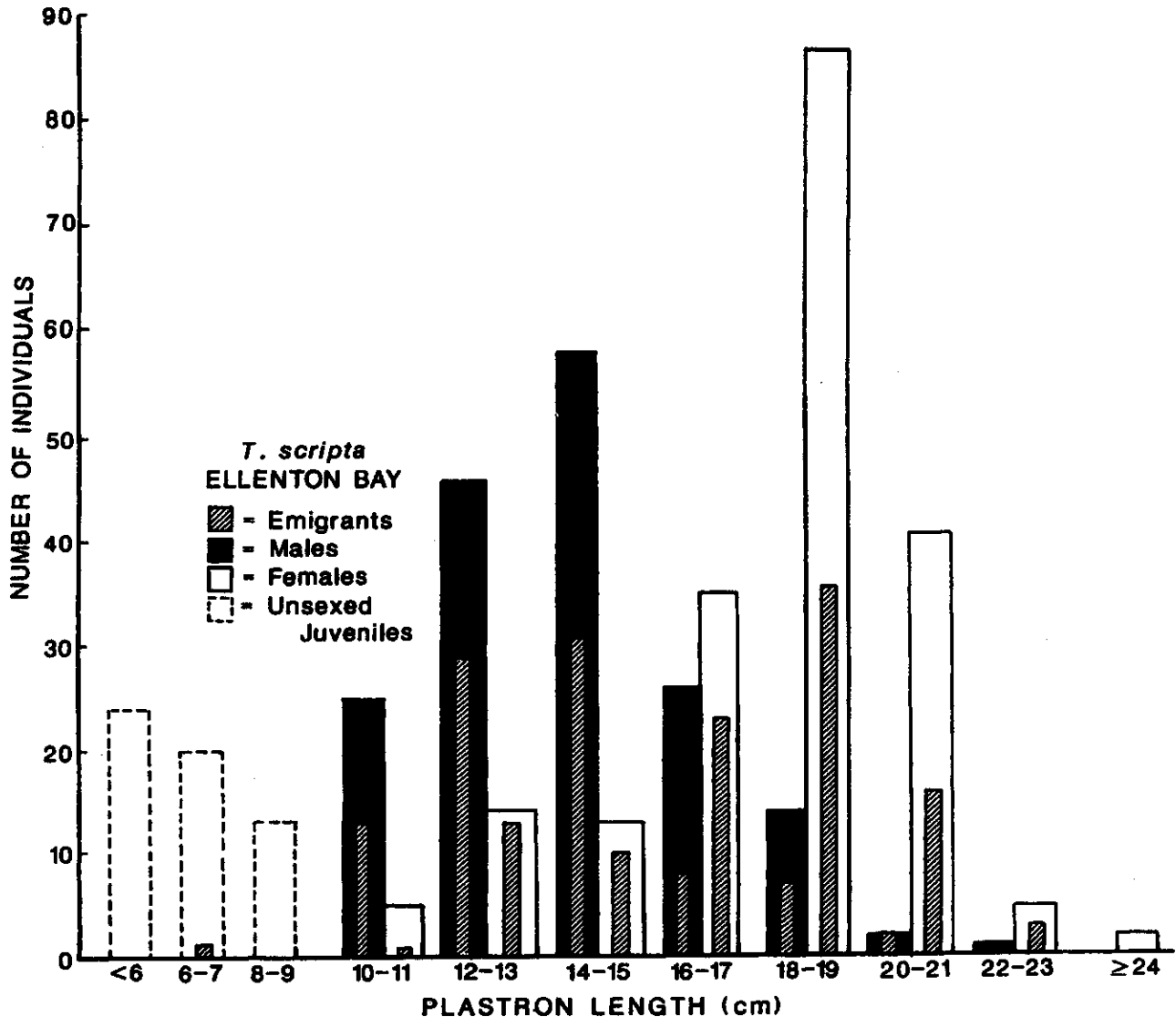


FIGURE 16.4. Extrapopulational movement by *T. scripta*, based on captures of individuals at drift fences during nondrought years at Ellenton Bay (1 January 1975–31 December 1978). The external bars represent the cumulative number of each sex and size class known to be present in the habitat during the annual sampling periods. The nested bars represent the numbers of each sex and size class that were captured exiting the aquatic habitat and that did not return during the year of departure. An individual turtle may be included more than once, because the purpose is to compare what proportion of a size class exited in a year with the number available. Hatchlings were not included in the juvenile samples.

.01, $\chi^2 = 37.03$, $df = 4$), nor were the directions chosen by females within any of the species (Fig. 16.5). Nonetheless, the choice of nesting direction by an individual on a subsequent trip was most likely to be in the same direction as its previous trip (Tables 16.3 and 16.4).

The explanation for these particular observations is that the terrestrial habitat surrounding Ellenton Bay is relatively homogeneous, so a nesting female turtle can depart from the aquatic habitat in any of several directions without a preconception that some directions are unsatisfactory for nesting. Once a female has nested safely, it would not be surprising to find that she tends to

travel toward the same area to seek a suitable nesting site in the following year. The risks associated with terrestrial travel can be great, and a nesting individual would be expected to follow a known route that resulted in her own survival and a satisfactory nest on a previous occasion, rather than to wander randomly during each nesting bout.

Although the consistency of females in their direction of departure was high, variability in the direction of departure was observed among some females at the Ellenton Bay drift fence and may be a consequence of several factors directly associated with nesting biology. For example,

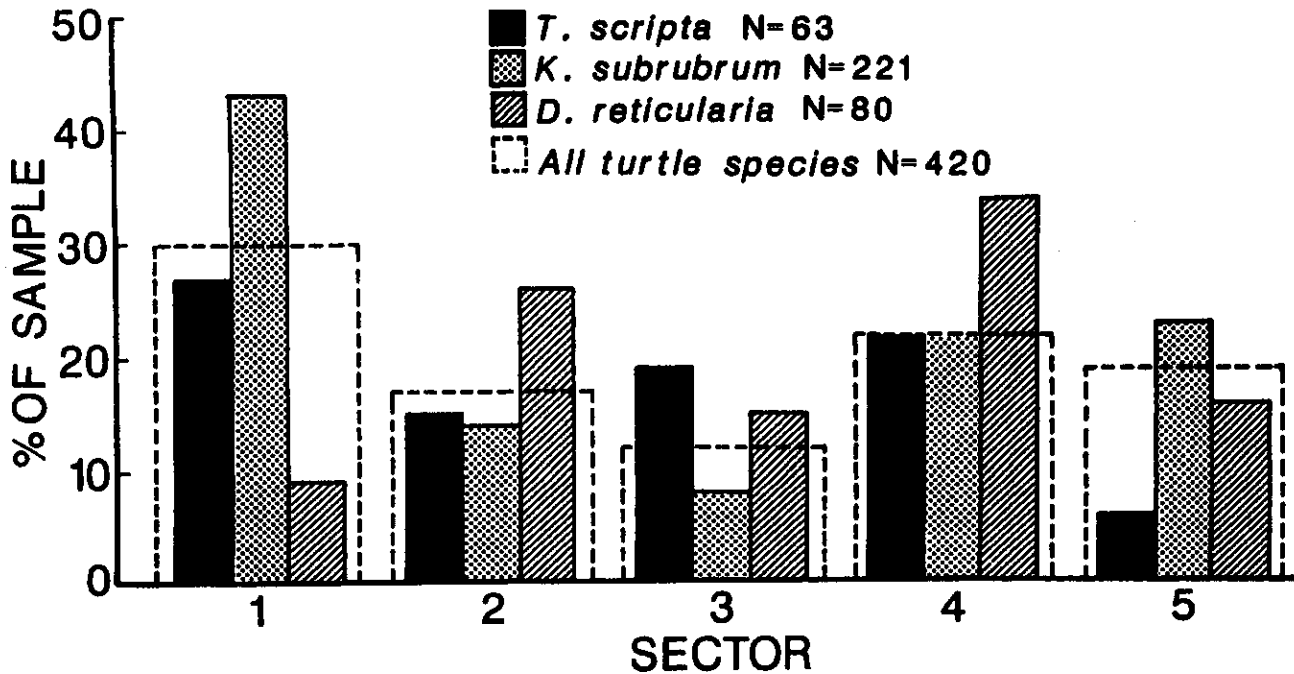


FIGURE 16.5. Direction of departure of nesting females of three species from Ellenton Bay. Each sector represents approximately 250 m of drift fence with pitfall traps (see Fig. 2.4) that completely encircled the aquatic habitat. Hence, sectors 1 and 5 are adjacent. Only females known to be carrying eggs, based on x rays, palpation, or eventual nesting activity, were used in the analysis. In addition to including the samples of *T. scripta*, *K. subrubrum*, and *D. reticularia*, the total sample includes *S. odoratus* ($N = 28$), *P. floridana* ($N = 22$), and *C. serpentina* ($N = 6$).

a female may have chosen a marginal site because of particular circumstances of physiology, environmental conditions, and timing. In the following year, the same female may choose to exit the aquatic habitat in a different direction in search of a more favorable nesting site. Another possible cause of a female's changing her direction of departure from the aquatic habitat is that although she left in a particular direction on the previous nesting excursion, she wandered extensively before finding a nesting

location, and then returned to the aquatic habitat from a different direction. Therefore, on her next departure for nesting purposes she might leave in the direction of the previous nesting site. The extensive efforts to track nesting female freshwater turtles on the University of Michigan's E. S. George Reserve should be a major source of enlightenment about this critical yet poorly understood phase in a turtle's ecology (Congdon et al., 1983b, 1987).

Table 16.3. Consistency of direction of departure by nesting females of three species of freshwater turtles captured in different years

Species	Relationship between sectors of first and second captures		
	Same	Adjacent	Opposite pair
<i>Trachemys scripta</i>	6	4	2
<i>Kinosternon subrubrum</i>	34	7	4
<i>Deirochelys reticularia</i>	4	6	3
Total	44	17	9

Note: The sector of the second nesting event of an individual nesting in a subsequent year was compared with the sector of the first event. Thus, each individual is represented only once. Multiple nesting events are indicated in Table 16.5, and those individuals are not included here. Sectors and methods of identifying nesting females are explained in Figure 16.5. Sectors 1 and 5 are adjacent.

DEPARTURE FROM AN UNSUITABLE HABITAT

Animal populations are commonly confronted with conditions that are less than satisfactory. When conditions become untenable because of environmental extremes, individuals take compensatory measures that may not influence others in the population. Two general adaptations are apparent among species that have evolved in habitats that can sporadically become unsuitable for continued inhabitation. One approach is to remain in the habitat in a quiescent state. The other is to leave in search of a better situation. Freshwater turtles have evolved both strategies.

Cagle (1944b) observed extrapopulational movement by *Chrysemys picta* and *T. scripta* in response to the drying of a lake, and Hamilton (1944) recounted a migration of *G. berlandieri* that were assumed to be leaving a flooded habitat. Parker (1984) reported that *T. scripta* emigrated

Table 16.4. Sectors from which Ellenton Bay egg-carrying females departed in three or more years from 1976 to 1987

Species	Number of individuals	Individuals nesting in same sector for three or more consecutive years	Individuals nesting in same or adjacent sector for three or more consecutive years
<i>Trachemys scripta</i>	3	0	2
<i>Kinosternon subrubrum</i>	21	16	20
<i>Deirochelys reticularia</i>	9	2	7

Note: If an individual nested more than once in a particular year, the sector of the first nesting excursion for that year was used. Sectors 1 and 5 are adjacent. Sectors and methods of identifying nesting females are explained in Fig. 16.5.

from a farm pond where an algicide was used that eliminated their primary food source. Gibbons et al. (1983) documented an emigration by a large segment of the populations of *T. scripta* and *P. floridana* from Ellenton Bay in the direction of the nearest body of water during an extreme drought. *Kinosternon subrubrum* and *D. reticularia* did not leave Ellenton Bay during the same drought, nor did *Chelydra serpentina* leave the drying lake observed by Cagle (1944b). Cahn (1937) concluded that a large number of *Chrysemys picta* died because they failed to leave a drying lake in Illinois, in contrast to those observed by Cagle (1944b).

Ellenton Bay data permit examination of the survival aptitude of freshwater turtles confronted with conditions in which their habitat became untenable for an aquatic existence. Ellenton Bay dried completely or almost so during the summers of 1968, 1981, and 1985 (see Chapter 2), but during the intervening years, turtles were active in the aquatic habitat. One or more individuals of each of the six species lived through each of the major droughts. Some individuals of *T. scripta* ($N = 5$) and *K. subrubrum* ($N = 7$) lived successfully through all three droughts (Table 16.5). These observations indicate that both extrapopulational movement (*T. scripta*) and quiescence (*K. subrubrum*), two entirely different strategies, can be effective for some individual turtles.

To understand further how some species of turtles respond to unfavorable habitat changes, we conducted an experiment in which Risher Pond was fenced and then drained, and the response of turtles occupying the pond was observed. The pond was completely enclosed by a drift fence with pitfall traps from January 1969 to January 1971. The fence was reestablished in January 1984. All movements by turtles into or out of the aquatic area were monitored in each of these years. In the summer of 1984 the pond was drained.

In the five months before the pond was drained, only 79 turtles, including nesting females, had left the habitat. During the few days that the water level was lowered (15–22 July 1984), 120 turtles emigrated (Table 16.6). *Kinosternon subrubrum* and *Chelydra serpentina* did not leave in

response to the draining, although both were present in the pond. As was noted above, *C. serpentina* have been reported to bury themselves in the mud under such conditions (Cagle, 1944b), and *K. subrubrum* did not emigrate from Ellenton Bay in greater than usual numbers during a drought (Gibbons et al., 1983). In contrast to our earlier observations at Ellenton Bay, *D. reticularia* responded to the abrupt drop in water level by emigrating. Perhaps the rate of drying of an aquatic habitat can be highly influential in determining the response of some species to falling water levels.

EXTRAPOPULATIONAL MOVEMENT OF MALES

Some long-distance movements reported for adult turtles are apparently unrelated to nesting or seasonal environmental changes. The explanation for many of these observations may lie in the tendency of adult males of a polygynous species to move extensively in search of mating opportunities with receptive females (Gibbons, 1986). The highest reproductive success should be achieved by male turtles that encounter and mate with the most females, even though adult males that engage in long-distance travel would undergo greater risks and incur higher energy costs associated with movements than turtles that remain in a habitat. Adult female turtles would be expected to have less potential fitness gain from multiple mating encounters than would males. Presumably a single mating is sufficient to fertilize a clutch of eggs, but in addition female turtles are capable of storing sperm and producing fertile eggs for up to four years after mating (see Chapter 9). This would further lessen any tendency for females to take unnecessary risks in search of mating encounters. Males, therefore, would be expected to be more active than females or immature males, moving longer distances and more often in search of mates. The extent of the mating season has not been carefully defined for most species of turtles but is a critical factor in this phenomenon.

The period of greatest sexual activity of *T. scripta* is presumed to be from fall to spring (approximately late

Table 16.5. Number of individuals of six freshwater turtle species that survived major droughts and total drying of the aquatic habitat at Ellenton Bay

Species	Sex	Number captured before drought year			Number recaptured		
		1967-68	1969-81	1982-85	After 1968	After 1981	After 1985
<i>Trachemys scripta</i>	M	150			38	1	4
	F	150			52	1	1
	J	115			11	0	0
	M		417			33	29
	F		412			22	48
	J		329			6	1
	M			62			8
	F			45			4
	J			27			1
<i>Kinosternon subrubrum</i>	M	73			19	3	3
	F	96			26	1	4
	J	12			0	0	0
	M		298			25	43
	F		219			10	49
	J		89			4	0
	M			80			11
	F			55			5
	J			24			1
<i>Deirochelys reticularia</i>	M	73			13	0	0
	F	38			7	0	0
	J	15			2	0	0
	M		134			16	5
	F		85			3	2
	J		222			1	1
	M			23			1
	F			9			0
	J			8			0

Table 16.5 -- Continued

Species	Sex	Number captured before drought year			Number recaptured		
		1967-68	1969-81	1982-85	After 1968	After 1981	After 1985
<i>Sternotherus odoratus</i>	M	27			0	1	0
	F	24			4	0	0
	J	1			0	0	0
	M		78			1	0
	F		67			1	0
	J		22			1	0
	M			9			0
	F			2			0
	J			4			0
<i>Pseudemys floridana</i>	M	5			3	0	0
	F	8			4	0	0
	J	9			0	0	0
	M		54			2	2
	F		60			2	4
	J		70			0	0
	M			2			0
	F			4			0
	J			3			1
<i>Chelydra serpentina</i>	..*	3			2	0	0
	M	3			1	0	0
	F	0			--	--	--
	J	3			0	0	0
	M		23			2	1
	F		9			2	2
	J		76			1	1
	M			7			0
	F			3			1
J			7			0	

Note: Recaptures in the after-1981 and after-1985 categories are not included in earlier categories. Abbreviations: M, adult males; F, adult females; J, juveniles. *Unsexed adults.

Table 16.6. Emigration of aquatic turtles in response to draining of Risher Pond in 1984

Species	Jan. 1969-Jan. 1971				1 Jan.-15 July 1984				15-22 July 1984 (draining of pond)			
	M	F	J	Total	M	F	J	Total	M	F	J	Total
<i>T. scripta</i>	7	16	8	31	2	12	3	17	4	6	15	25
<i>K. subrubrum</i>	32	29	7	68	1	10	3	14	3	--	4	7
<i>D. reticularia</i>	9	10	11	30	1	10	3	14	4	3	20	27
<i>S. odoratus</i>	3	10	1	14	7	9	1	17	--	9	11	23
<i>P. floridana</i>	1	3	5	9	2	12	3	17	18	--	20	38
<i>C. serpentina</i>	3	6	2	11	--	--	--	--	--	--	--	--
Total	55	74	34	163	13	53	13	79	32	18	70	120

Note: Numbers indicate turtles leaving the lake, as measured by captures at a drift fence during different times. Abbreviations: M, males; F, females; J, juveniles.

September to early April) in South Carolina, although actual observations of courtship and copulation are rare (see Chapter 9). Slider turtles will apparently mate during the winter if temperatures are warm enough for activity. Springtime mating is assumed for *K. subrubrum*, but fall breeding may also occur, as in *Sternotherus odoratus* (McPherson and Marion, 1981a). The reproductive pattern of *D. reticularia* seems at variance with all other U.S. species. Female chicken turtles lay eggs from September to March (Gibbons and Greene, 1978), the exact period when other species do not lay eggs.

Few investigators have considered the differential behavior patterns of the sexes within turtle populations. Adult female *Chrysemys picta* were found to move significantly greater distances in the Sherriff's Marsh population in Michigan than were adult males (Gibbons, 1968d), presumably because the large and continuous aquatic habitat resulted in females' traveling long distances to find suitable nesting sites and then returning to the nearest aquatic area, not necessarily the area from which they had departed. In *T. scripta* populations adult males have been reported as characteristically making most of the lengthy overland excursions and being active during a greater portion of the year than are females (Morreale et al., 1984; Parker, 1984; Gibbons, 1986). Among terrestrial turtles, Rose and Judd (1982) noted larger home ranges for males than for females in *G. berlandieri* populations. All of the transient box turtles (*Terrapene carolina*) that made long-distance movements exceeding the distances normally moved by other members of the population were males (Kiester et al., 1982). Male *Clemmys marmorata* in a population studied by Bury (1972) had significantly larger home ranges than did females.

In comparing extrapopulation movement patterns of the sexes, several spatial and temporal measurements permit quantification of different movement patterns and provide means of testing the hypothesis that adult males move more frequently and greater distances during the mating period than females and juveniles, presumably to increase mating probabilities. As is indicated in Figure 16.1, male *T. scripta* on the SRP moved farther than females, based on recaptures at different sites. Turtles from the A-Area Seepage Basins give additional confirmation of differential movement by the sexes, with females apparently being more sedentary (Fig. 16.3).

During nondrought years, adults of both sexes of *T. scripta* made more extrapopulation moves than did juveniles, although a few immature females above 120 mm in plastron length were registered leaving the aquatic habitat (Fig. 16.4). Of 172 adult males (cumulative over four years) present and potentially capable of leaving Ellenton Bay, 95 (55%) exited during a year and did not return; of 168 adult females, 76 (45%) failed to return (Fig. 16.4). Most of the exits from aquatic areas by female *T. scripta* are during the spring (Table 16.7). The

Table 16.7. Seasonal extrapopulation movement by adults of five species of freshwater turtles at Ellenton Bay

Species	Season	Out		In	
		Male	Female	Male	Female
<i>T. scripta</i>	Winter	7	5	3	8
	Spring	154	191	70	85
	Summer	50	41	56	68
	Fall	165	4	7	8
<i>K. subrubrum</i>	Winter	7	1	25	10
	Spring	54	178	128	203
	Summer	39	112	40	137
	Fall	122	84	13	14
<i>D. reticularia</i>	Winter	4	20	1	9
	Spring	67	85	47	78
	Summer	24	25	32	16
	Fall	31	32	4	11
<i>S. odoratus</i>	Winter	0	0	0	1
	Spring	8	51	3	27
	Summer	19	8	16	120
	Fall	6	0	4	2
<i>P. floridana</i>	Winter	1	0	1	0
	Spring	22	16	4	7
	Summer	11	28	5	31
	Fall	4	0	4	2

Note: Records are based on captures in all nondrought years. Those reported as exiting were individuals that did not return to the aquatic habitat during the year. Those entering were first captures of the year. Entering hatchlings and other juveniles are excluded.

majority of the females are leaving to nest, although whether their failure to return is primarily a consequence of predation or emigration to another site is unresolved. Therefore, many of the departures by females may have been made with the intention of returning after nesting, whereas the departures by males were presumably for the purpose of reaching another habitat. The high incidence of springtime exiting and entering of aquatic habitats by both sexes, especially males (Table 16.7), may represent overland movement from other aquatic sites.

With the exception of data on nesting females, these observations of terrestrial activity do not confirm the purpose of the extrapopulation movement. The departure of immature females suggests that a search for more favorable habitat may be involved. Eighty-nine percent (24 of 27) of the immature females with plastron lengths ranging from 120 to 159 mm, and only 62% (64 of 104) of the adult males in those size classes, were last captured exiting Ellenton Bay in one or more of four years (Fig. 16.4), indicating that other factors may be involved in the departures of individuals from the aquatic habitat.

Temporal Activity

The objective in determining when turtles move is to relate movement to predictable changes that occur on a

daily and seasonal basis, intrinsic factors such as hunger and state of maturity, and unpredictable environmental factors such as flooding and drought. The responses of individuals in populations to particular conditions are undoubtedly a consequence of the interaction of all three factors. Some of these have been discussed in earlier sections. Diel and seasonal activity patterns are discussed below.

DIEL ACTIVITY PATTERNS

The slider turtle contains a diurnal activity pattern throughout its geographic range, as far as is known. The studies on the SRP can contribute little to the knowledge of diel activity patterns of the slider or other species of turtles, beyond the categorical statement that freshwater turtles on the SRP do not travel overland during darkness, nor do they appear to be active aquatically at night. SREL personnel have spent hundreds of hours collecting reptiles and amphibians on highways at all hours of the day and night and during all seasons. No turtle has ever been collected on a highway during darkness, although large numbers have been collected crossing roads during the daytime. Nighttime observations of slider turtles in the water have not revealed them to be active at night except in response to disturbance by a collector. Those seen at night are normally underwater on the surface of the mud or buried beneath the substrate, but some species are active nocturnally in the water. Some sea turtles characteristically nest at night (Carr, 1952; Ernst and Barbour, 1972), and individuals of some freshwater species have been reported to nest at night on some occasions, although other individuals of the same species nest during the day (Congdon et al., 1983b, 1987).

SEASONAL ACTIVITY PATTERNS

Spring is the period of greatest terrestrial activity for both sexes of most species observed on the SRP. We have little information on how aquatic intrapopulational movement varies seasonally, but we assume that the high level of travel across the land-water interface indicates an overall level of activity. The adult activity patterns of certain species are revealed in an examination of observed terrestrial activity (Table 16.7). For example, *K. subrubrum* shows high activity in summer and fall, indicating the departure of individuals to hibernation areas, and a high entry into the aquatic habitat as they return in the spring. The observations of *D. reticularia* reveal the fall and winter nesting of females. Male emigration activity is higher in the fall than in the summer and perhaps indicates a fall breeding period. Clearly, additional studies must be conducted to quantify and understand these activity cycles.

HIBERNATION AND ESTIVATION

Many species of turtles migrate significant distances in response to seasonal changes to hibernate and estivate. We use the traditional and straightforward definitions that hibernation is dormancy during winter, and estivation is dormancy during summer or drought. All turtles in cold temperate zones hibernate. Estivation appears to be a common, though less predictable or perhaps less well-documented, phenomenon in areas with seasons that are hot and dry.

Hibernation is essential for turtles living in regions where winter temperatures approach or fall below freezing. Freshwater turtles that live in larger bodies of water are buffered from thermal extremes by the water itself, and many simply retreat into the mud or under the bank to wait out the colder periods. Many species in South Carolina that remain in aquatic areas become active on sunny days if their body temperatures can be raised sufficiently by aquatic or aerial basking. The risks to survival during winter from inaction are obviously of sufficient magnitude that they outweigh the risks encountered in overland or aquatic travel by freshwater species to hibernation sites. Thus, extrapopulation migration to and from hibernation sites is a common occurrence in many species of turtles.

Netting (1936) concluded that spotted turtles (*Clemmys guttata*) traveled in the spring from an upland hibernation site to a low-lying area. Painted turtles (*Chrysemys picta*) on the E. S. George Reserve left shallow marsh areas and retreated to deeper hibernation ponds during fall (Sexton, 1959b). After winter they returned to the shallow, vegetated areas. Adult mud turtles (*K. subrubrum*) on the SRP leave aquatic habitats during fall to overwinter on land, sometimes more than 1 km from water (Bennett et al., 1970).

Seasonal movements to avoid cold temperatures occur among sea turtles, which migrate toward tropical waters during winter. For example, leatherback sea turtles (*Dermochelys coriacea*) have a wide oceanic distribution in which individuals observed at high latitudes during warmer months of the year presumably return to equatorial waters during winter (Pritchard and Trebbau, 1984). Among terrestrial species, *Gopherus agassizii* have been reported to move to hibernaculum sites (Woodbury and Hardy, 1948), although the locations were apparently not far from their summer feeding areas.

Long-range seasonal movement patterns by freshwater turtles have been observed by means of the Ellenton Bay drift fence and pitfall traps. These observations have revealed only one species in the region (*K. subrubrum*) to display extrapopulational migration for hibernation consistently (Bennett et al., 1970). Although large numbers of *T. scripta* and *Pseudemys floridana* departed from Ellenton Bay during a period of extreme drought (Gibbons et al.,

Table 16.8. Seasonal entry of hatchling freshwater turtles to aquatic habitats

Species	Month											Total
	J	F	M	A	M	J	J	A	S	O	N	
<i>T. scripta</i>		2	110	46	8	7		4	3	1		181
<i>K. subrubrum</i>		29	358	118	15	7	3					530
<i>D. reticularia</i>			143	114	3	3		2	6			271
<i>S. odoratus</i>			6	2	1	5	1	2	6		1	24
<i>P. floridana</i>			33	51	9	9	1			1		104
<i>C. serpentina</i>	1		1	1	2	1			6			12
Total	1	31	651	332	38	32	5	8	21	2	1	1,122

Note: Figures are based on pitfall trap captures on the SRP from 1968 through 1987. No hatchlings were captured during December of any year.

1983), this is not an annual occurrence with these species, whereas *K. subrubrum* characteristically leaves in late summer or fall and returns when spring arrives (Table 16.7).

Observations of *T. scripta* in Ellenton Bay during wet years when winter water levels have been high indicate that this species will remain in the aquatic habitat for hibernation. This is also true at Risher Pond, Par Pond, and Pond B, where turtles have been captured in the water during December, January, and February (Par Pond, $N = 166$; Pond B, $N = 92$; Risher Pond, $N = 9$; Ellenton Bay, $N = 58$). It is possible that *T. scripta* in some situations may move to particular areas for hibernation, as observed in *Chrysemys picta* by Sexton (1959b). However, no evidence has been presented to suggest that *T. scripta* does anything other than respond individually to the onset of cold by finding a safe retreat in the area of normal activity.

MOVEMENT TO AREAS WITH DIFFERING RESOURCES

Aside from activities associated with hibernation or other responses to winter conditions, many animals move long distances seasonally in response to changing food resources or other nutrient requirements. It is conceivable that some turtles may make determined travels beyond the limits of the normal population habitat to acquire a predictable resource in another area. Desert tortoises are known to travel to specific sites to eat soil, presumably to acquire required nutrients that are not in sufficient quantity in their normal diet (Kristin Berry, pers. com.). Some individual tortoises may have to travel long distances outside their usual activity area to achieve this objective, but they would have to have made such a trip already without any assurance of finding the resource, because they could not have known of it initially.

Certain circumstances could lead to a generalized searching behavior in a population. For example, an Al-

dabra tortoise exposed to ultimately lethal conditions of overheating would be expected to set out in search of shade (Swingland and Lessells, 1979). Once a satisfactory spot is found, it may be used on a regular basis thereafter, even if it is a long distance from normal feeding areas.

Although seasonal diet shifts probably occur in several species of turtles, and some sea turtles make significant migrations from nesting beaches to feeding areas (Carr and Coleman, 1974; Mortimer, 1981), we are aware of only one observation in which major segments of a population of freshwater turtles actually make annual, long-distance movements during the normal activity period to capitalize on a particular food resource. Moll and Legler (1971) observed seasonal shifts in the activity area of tropical *T. scripta* in response to rainfall patterns, presumably because of the predictable availability of resources. An initial prediction for the unusual situation at Par Pond, the large reservoir receiving thermal effluent on the SRP, was that slider turtles would follow the thermal gradient and move from the colder regions of the lake to the warm end during winter, where feeding could occur almost year-round. Such a concentration phenomenon has been observed in American alligators (Murphy and Brisbin, 1974) and largemouth bass (Gibbons et al., 1978a) but was not documented to occur in turtles (Schubauer, 1981a).

If predetermined habitat shifts by turtle populations are discovered, they will most likely occur in aquatic species occupying large bodies of water, such as rivers, where detectable gradients exist that would provide cues to all individuals in the population about available resources in another area. It is unlikely that annual migrations would develop among the many species that occupy temporary aquatic habitats and that rely on extensive overland travel. Under most circumstances, movement to capitalize on food resources that vary seasonally in different areas is most likely to be a consequence of individual experience and chance, not a population phenomenon.

MOVEMENT OF HATCHLINGS FROM NEST TO WATER

The initial movement by all species of aquatic turtles is the overland trip from the nest to the water, the entry into the population. The hatchling movement per se need not be discussed in terms of benefit to the individual, for indeed the trip is one of necessity. However, the seasonal timing of nest departure varies among species, and whether hatchlings leave the nest soon after hatching or overwinter in the nest (Gibbons and Nelson, 1978) has presumably been influenced by natural selection on the basis of the risks and benefits of the timing.

The turtles belonging to five of the six species that inhabit Ellenton Bay generally lay eggs in the late spring (*Deirochelys reticularia* nest in fall, winter, or early spring; see Chapter 9), and the hatchlings enter the water about a year later (Table 16.8). However, high variability in the seasonal timing occurs in every species, and at least a small proportion of most species apparently emerge soon after hatching, without overwintering. For most species of turtles the risks associated with immediate emergence

seem to outweigh those of a delayed emergence, which may double the amount of time in the nest. A careful look at how risks vary among species, years, and habitats would be instructive in addressing the question of why turtles emerge from the nest when they do, and such risks should become a focus of studies on hatchling emergence phenomena.

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