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# PROMOTION OF GENE FLOW BY TRANSIENT INDIVIDUALS IN AN OTHERWISE SEDENTARY POPULATION OF BOX TURTLES (*TERRAPENE CAROLINA TRIUNGUIS*)

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Recent theoretical work in population genetics has suggested an important role for occasional long-distance migrants in maintaining genetic similarlity between populations and in aiding the spread of advantageous genes (Slatkin, 1976; Slatkin and Charlesworth, 1978). This result is in contrast to some earlier models (e.g., Fisher, 1937) but as Slatkin (1976) states it is "unfortunate in some ways since the frequency of rare, [reproductively] successful, long distance migrants is extremely difficult to measure." Discovery of three long-distance breeding migrants in a population of usually sedentary box turtles provides an example of a species in which a few individuals could greatly enhance gene flow. These transients also demonstrate that box turtles are behaviorally capable of unidirectional long-distance movement. Further, they underscore the methodological difficulties of detecting individuals contributing to long-distance gene flow in populations (see also Ehrlich and Raven, 1969).

Several authors have speculated on the existence of true transients in box turtle populations (Stickel, 1950; Legler, 1960; Williams, 1961; Dolbeer, 1969). By transient we mean that a turtle moves more or less continuously through the environment without recrossing any of the areas it has passed through previously. Such animals are in contrast to those which possess a home range within which all activity is confined. Although there has been some indirect evidence that transients exist, direct confirmation has not previously been possible.

We report the existence of true transients in a three-toed box turtle (*Terrapene carolina triunguis*) population. These animals were detected in the course of a 16-year study on a population located on a 32.4-hectare study site in Cole County, Missouri (Schwartz and Schwartz, 1974; Kiester et al., unpubl.). This ongoing study consists, in part, of an extensive mark-recapture program. Estimates from the Jolly-Seber stochastic mark-recapture model (Seber, 1973 p. 196–232) indicate that over 70% of the population is marked at any one time and that the size of the population varies between 400 and 600 individuals. The majority of the population is sedentary with individuals occupying home ranges of less than 2 hectares. This result accords with previous studies on this species (Nichols, 1939; Stickel, 1950; Dolbeer, 1969; Schwartz and Schwartz, 1974; Yahner, 1974; Madden, 1975). Of 359 individuals marked on the area in 1965, 32 were recaptured again in 1980. Of 193 marked in 1966, seven were recaptured in 1980. The average annual probability of survival as estimated by the Jolly-Seber method is 0.82 (standard deviation = 0.06, $N = 14$). Thus many turtles remain in the study area for considerable periods of time. Other studies have found resident individuals persisting for up to 30 years (Stickel, 1978).

In 1976 we began intensive radio-tracking studies with the following protocol. Five turtles that were first captured on the study area in 1965 were radio-tagged and their movements followed. These were considered a control group and their home range size was found to be similar to that estimated by the mark-recapture study (Schwartz and Schwartz, 1974). Other radios were placed on seven animals caught in 1976 for the first time as adults in the central section of the study area. Because of the intensity of the mark-recapture program the probability is extremely low that these individuals had grown up in the study area but had escaped detection. Of the seven turtles which met this criterion and were tagged and followed for any length of time, three turned out to be transients while the others were found to have home ranges just outside the boundary of the study area. Figure 1 is a map of the routes traveled by these three individuals. All three were adult males. Number 8071 (140 mm carapace length, minimum estimated age 10 yr) was followed from 1 May 1976 to 4 July 1977 and provided the most remarkable record of long-distance movement. This individual travelled a total straight-line distance of approximately 10.0 km. It is of interest to note that it resumed its course after hibernating from 31 October 1976 to 12 April 1977. Number 1273 (131 mm carapace length, minimum estimated age 25 yr) was followed from 24 May 1977 to 8 May 1978. This individual remained in a 2-hectare area on the study site from 24 May 1977 until 28 August 1977 when it struck out on the path indicated in Figure 1. It moved a straight-line distance of 1.9 km and was followed into hibernation in early November 1977, and lost upon emergence the next spring (8 May 1978). Number 1299 (130 mm carapace length, minimum estimated age 12 yr) was followed from 26 July 1977 to 14 September 1977 and covered a distance of 2.8 km. All three individuals moved through a wide variety of habitats ranging from oak-hickory forest through many second growth and weed habitats to several man-made habitats such as crop fields and backyards. Movement tended to be in a straight line regardless of features of the landscape. On several occasions number 8071 moved up a creek bed for some distance but then moved out of the shady wet habitat into open fields despite the fact that this was during the hot and dry part of June and July. Movement was not continuous, especially during the hotter and drier parts of the summer, but in bouts of one or two days following one or two days in a small area. Backtracking was uncommon and rarely for more than a few dozen meters.

Number 8071 was found mating with female turtles on two occasions during the course of the study and within 1 m of a female on four other occasions. Number 1273 was found mating three separate times during the course of its movement. This frequency of mating is similar to that found for individuals in the sedentary population.

These cases demonstrate that box turtles are capable of long-distance oriented movement. Several studies (Nichols, 1939; Gould, 1957; Lemkau, 1970; Madden, 1975) have shown that this species is capable of oriented movement over distances less than 1 km, although the mechanisms by which this is accomplished are not known (Madden, 1975; Carroll and Ehrenfeld, 1978). Whatever these mechanisms are, it is clear that this species shows a broad, if not bimodal, distribution of movement distances.

These results imply that the population structure of this species is not greatly subdivided as would be supposed if all individuals had small home ranges on the order of 150 m in diameter. Even if transients constitute only a small fraction of the population, population genetics theory (Wright, 1969 p. 290–344) indicates that the species would not be genetically subdivided except on a scale much larger than the usual migration distance. For a selectively neutral allele in a continuous population, Malecot (1969 p. 64–74) has shown that the distance over which two local populations can be expected to have the same alleles is a function of the variance in individual migration distances. In particular, if the migration distances are bimodally distributed, this will substantially increase the variance and the distance over which populations will be correlated. On the other hand, well-marked subspecies do exist in this species (Carr, 1952 p. 137–156), indicating that the species is by no means panmictic.

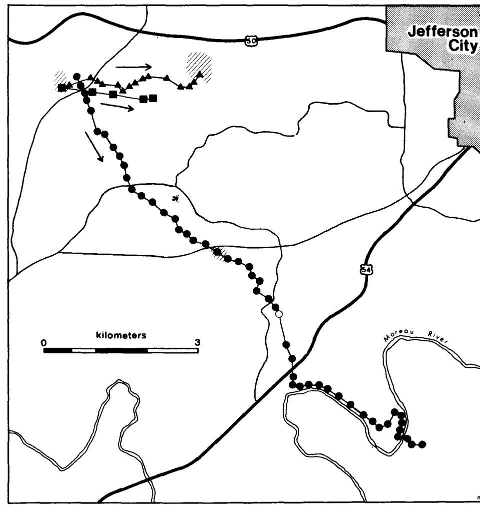


FIG. 1. Routes traveled by three transient box turtles through Cole County, Missouri. Circles, Number 8071; squares, Number 1273; triangles, Number 1299. Arrows indicate direction of movement away from the study site. Hatching indicates areas where recrossing of paths occurred. Hollow circle locates the hibernation site of 8071. Note hesitation of Number 8071 before crossing the Moreau River. Turtles were followed using radio transmitters (A.V.M. Instruments Co., Champaign, Ill.) which were attached to the rear of the shell and did not interfere with the movements of the turtles in any way.

These results underscore an important point: most population studies are methodologically blind to the existence of true transients. Any mark-recapture study on a fixed study site confounds transients both with individuals suffering mortality and with those individuals whose home range only partly overlaps the study site so that the probability of recapture given a capture is extremely low. On the other hand, because transients are not common in the population, it would require a very large number of radio-tagged turtles to pick up a transient. Our method, combining radio-tracking and mark-recapture, has a higher probability of detecting transients. It may be that such individuals occur in other species but have not been detected because of the methodological problems. Nonetheless, such individuals could be of great importance in understanding the evolution of these species.

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