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Interpond Movement Patterns of *Chrysemys picta picta* (Eastern Painted Turtles) in Virginia. Linnaeus Fund Research Report

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Population ecologists have traditionally focused on the dynamics of populations inhabiting single isolated habitat patches. However, in recent years, this focus has shifted to encompass the interaction of populations among several habitat patches. Levins (1970), in the first mathematical treatment of spatially subdivided populations, modeled regional population persistence as the interplay between local extinctions and subsequent recolonization. As such, Levins' metapopulation model is directly dependent on movement of individuals between habitat patches. Many spatially-explicit population models have been proposed since Levins' seminal work (reviewed in Harrison, 1991), but all have dispersal as the key element linking subpopulations.

Despite the perceived importance of dispersal, little empirical research has been devoted to determining the frequency and extent of movement between habitat patches. In a review of 415 papers concerned with spatially structured populations, only 68 (16%) have recorded number of interpatch movements (Bowne and Bowers, in press). Part of the problem is the difficulty of documenting interpatch movement (see review by Ims and Yoccoz, 1997). In the absence of empirical data, dispersal between patches is often assumed to be random or a function of isolation. As such, the size, shape, and position of habitat patches are believed to strongly affect the probability of an individual settling in a particular patch (Wiens et al., 1993; Fahrig and Merriam, 1994).

My research addressed this dearth of information by examining interpond movements of *Chrysemys picta picta* (eastern painted turtles) in Virginia. Movement between ponds by *C. picta* has been reported in several studies. Zweifel (1989) reported age and sex-specific interpond movements in New York and noticed an increase in movement by males upon sexual maturity. Sexton (1959) observed seasonal migration between marshes in Michigan, in which adults made the journey more often than juveniles and females more than males. Similar seasonal movements were observed in Nebraska (McAuliffe, 1978) and in Illinois (Cagle, 1944). In contrast, several studies found little evidence of interpond movement (Gibbons, 1968; Bayless, 1975; Mitchell, 1988). This difference may be attributed to characteristics of the system studied. Interpond movement did not occur in systems with isolated ponds but did occur when several ponds were in close proximity (ca. 1 km).

The distance between ponds has a potentially large influence on observed patterns of interpond movement and subsequently on population distribution. With this in mind, I posed the following questions: 1) does the proportion of individuals that move between ponds differ by age/sex class, 2) what is the spatial extent of these movements, and 3) is the exchange of individuals most common between closest neighboring ponds?

Methods. — I conducted research at Blandy Experimental Farm (BEF) in Clarke County, Virginia, USA. BEF is located within an intensively managed agricultural landscape. Farm ponds located within this landscape provide ample habitat for *C. picta picta*. All ponds within a 3 km radius centered at BEF were included in the study. A maximum of ten ponds (actual number dependent on precipitation) within a single drainage in and around BEF formed the core of the study system (Fig. 1). These focal ponds were sampled for *C. picta picta* from May to September in 1998 (weekly) and 1999 (biweekly). Several neighboring ponds, all in other drainages, were occasionally sampled in 1999. Turtles were primarily captured with hoop traps (3 ft diam., 1 in mesh; Nylon Net Company, Memphis, TN) baited with sardines. Sex was recorded and individuals were given a unique identification code by filing marginal scutes. The length of plastron, right third foreclaw, and precloacal tail were measured with dial calipers and weight determined with a Pesola scale. Females with a plastron length of 106 mm or more were considered mature, which is the average size at maturity for females in a Virginian population (Mitchell, 1985). The elongation of the third foreclaw to 10 mm is indicative of sexual maturity in males (Gibbons, 1967; Frazer et al., 1993).

Three ponds (Rattlesnake Springs, Jones, and Center) within the focal area were potential destinations for emigrating turtles. The other seven ponds began to dry in late summer 1998 and did not receive immigrants. A movement event was said to have occurred the first time a turtle was captured in a pond in which it was not originally captured. Movements by turtles were initially classified as immigration to the "nearest, next nearest, and farthest pond." The null hypothesis of random movement between ponds by age/sex class (adult male, adult female, immature) was then analyzed using a 3 x 3 (3 destinations, 3 age/sex classes) chi square contingency table. Data on interpond movement were pooled across ponds to satisfy the average expected frequency requirement of this test (Zar, 1996). If random movement to the three ponds was rejected, then data were recategorized as movement to either the "nearest" or "non-nearest" pond and analyzed in a 2 x 3 (2 destinations, 3 age/sex classes) chi square contingency table. Rejection of the null hypothesis of random movement in this second contingency table would indicate that movement is either towards or away from the closest pond.

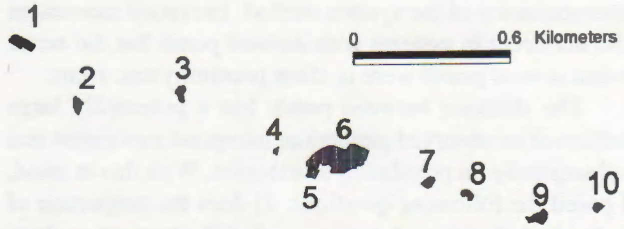

Figure 1. Distribution of ponds in focal study area at Blandy Experimental Farm, Clarke County, Virginia. Three ponds (1, 4, and 9) retained water over entire study period, all others dried in autumn 1998 and remained dry for 1999. Ponds: 1. Jones, 2. Cattle, 3. Georgette, 4. Rattlesnake Springs, 5. Arnold 1, 6. Arnold 2, 7. Drainage, 8. Border, 9. Center, 10. East.

Results. — A drought lasting from autumn 1998 to autumn 1999 severely impacted the study system. The ten ponds that formed the core of the study system in 1998 were reduced to three in 1999 (Fig. 1). Of the 332 recaptured turtles (547 total marked), 140 (42%) moved between ponds. Interpond movements varied by age/sex class (Table 1). Males moved most often (50%, 42 of 83 recaptured) followed by females (43%, 42 of 98 recaptured) and immatures (37%, 56 of 151 recaptured). The vast majority of movements between ponds covered distances of less than 0.9 km (Fig. 2). The maximum distance moved within the focal area was 1.4 km. Five individuals (4 adult males, 1 adult female) dispersed to ponds outside of the study system and moved between 1.7 and 2.4 km.

The hypothesis of random movement was rejected using a 3 pond x 3 age/sex class contingency table ($\chi^2_{0.05,4}$ = 106.5; $p < 0.05$). Very few turtles traveled to the most distant ponds. Therefore, data on immigration were collapsed into "nearest" and "non-nearest" categories. The hypothesis of random movement was again rejected using a 2 pond x 3 age/sex class contingency table ($\chi^2_{0.05,2}$ = 28.1; $p < 0.05$). Visual examination of the data (Table 1) revealed that movement was towards the closest pond but this result was strongly influenced by the behavior of immature turtles. Separate chi square goodness-of-fit tests for each age/sex class resulted in the null hypothesis of random movement being rejected for immatures ($\chi^2_{0.05,1}$ = 24.6; $p < 0.05$) but not adult males ($\chi^2_{0.05,1}$ = 1.5; $p > 0.05$) nor adult females ($\chi^2_{0.05,1}$ = 2.0; $p > 0.05$). This result was strongly influenced by the behavior of turtles toward Rattlesnake Springs. Immature turtles moved to Rattlesnake Springs in keeping with its proximity, but both adult males and adult females tended to avoid it (Table 1).

Table 1. Transition matrix of individuals moving from pond of origin to pond of destination from 1998 to 1999 by age/sex class. Only one transition per individual is recorded. Fewer ponds of destination exist because of a drought in late 1998 through 1999.

Adult Males

Destination \ Origin	Jones	Cattle	Georgette	Rattlesnake	Arnold1	Arnold2	Drainage	Border	Center	East	Total
Jones	.	3	5	0	2	0	0	0	0	0	10
Rattlesnake	0	0	2	.	14	0	1	0	0	0	17
Center	0	0	1	0	8	0	1	2	.	3	15
Total	.	3	8	.	24	0	2	2	0	3	42

Adult Females

Destination \ Origin	Jones	Cattle	Georgette	Rattlesnake	Arnold1	Arnold2	Drainage	Border	Center	East	Total
Jones	.	3	13	0	1	0	0	0	0	0	17
Rattlesnake	1	0	1	.	4	0	0	0	0	0	6
Center	0	0	0	0	8	0	0	0	.	11	19
Total	1	3	14		13					11	42

Immatures

Destination \ Origin	Jones	Cattle	Georgette	Rattlesnake	Arnold1	Arnold2	Drainage	Border	Center	East	Total
Jones	.	9	3	0	0	0	0	0	0	0	12
Rattlesnake	0	2	10	.	22	0	0	0	0	0	34
Center	0	0	1	0	2	0	0	1	.	6	10
Total	0	11	14	0	24	0	0	1	0	6	56

Discussion. — This research is a first step towards examining the interaction between individual behavior and population dynamics at the landscape level. Movements of individuals between spatially distinct habitats can functionally link seemingly isolated populations. A large portion of this population of *C. picta picta* moved between nearby ponds. The impact of this movement on (sub)population dynamics has yet to be determined, but hint at possible population-level effects.

Chrysemys picta is most vulnerable to predation while on land (Wilbur, 1975). This cost of moving, coupled with the fairly long distances traversed in this system, suggests that survival rates may be lower in this system than in ones in which turtles move less. Future work will address this possibility. Predation risk and other costs of movement likely vary by age/sex classes. As such, behavior of age/sex classes should differ to minimize those costs. Immature turtles moved least often and to the closest pond. This finding agrees with the notion that terrestrial movement is most dangerous for immature turtles due to their small size (Stevenson, 1985; Frazer et al., 1991). In contrast, mature *C. picta picta* were not influenced by interpond distance within the landscape scale of this study, and may be responding to habitat quality. Superior habitats for adult males may be those in which receptive females are present in higher than average numbers. A greater proportion of adult males in this study made interpond movements than did the other age/sex classes. Increased movement by adult males is common in turtles and is hypothesized to maximize mating opportunities (Morreale et al., 1984; Gibbons et al., 1990). Adult females may be responding to habitats that increase reproductive output. This may explain the avoidance of Rattlesnake Springs in which the cool, clear, spring-fed water may be less desirable than the warm, turbid water of the other ponds. The effect of habitat quality is being addressed in additional work.

The movements documented in this report were undoubtedly affected by the drought. The question is to what degree. Movements were very likely motivated by rapidly lowering water levels. The fact that only one movement from a permanent pond (Jones) was documented reinforces this statement. However, seasonal drying of ponds is a common feature of the study system and so the degree of observed movement may be typical. The question then arises as to the advantage of leaving a permanent pond when

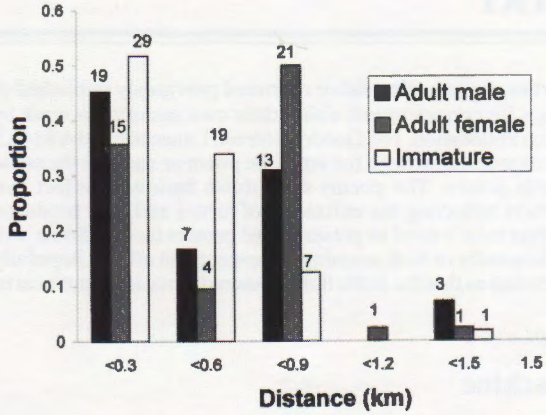

Figure 2. Proportion of recaptured *C. picta picta* that moved given distances between ponds by age/sex class. Each movement occurred over land. Number above each column represents absolute number of turtles per age/sex class traveling a given distance.

a potentially dangerous return trip is practically guaranteed. Several authors have suggested that turtles capitalize on the increased productivity of seasonal ponds during the growing season and then return to a more suitable overwintering site (Sexton, 1959; McAuliffe, 1978). However, to my knowledge, no one has compared fitness parameters (e.g., growth rates, reproductive output) between turtles that move into seasonal ponds and those that remain in permanent ones. My ongoing research also addresses this issue.

The five turtles that dispersed out of the study system may have important consequences for both population and genetic structure. These movements suggest that geographically and hydrologically separate ponds are functionally linked. The strength of this link will depend on the rate of exchange and the subsequent reproductive success of the dispersers. The observed rate of five turtles per year likely underestimates long-distance dispersal, as relatively little effort was devoted to sampling in the outlying ponds. In future work, I hope to more definitively address the rate of exchange and consequent effects on wider regional population dynamics.

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