

THE UNIVERSITY OF CENTRAL OKLAHOMA
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**Determining Population Boundaries and Densities of Red-eared Slider Turtles
(Trachemys scripta): An Empirical Field Test**

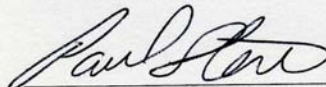
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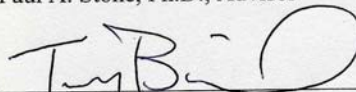
Determining Population Boundaries and Densities of Red-eared Slider Turtles

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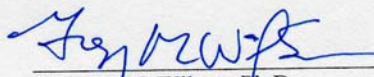
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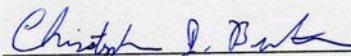
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ABSTRACT

Source-sink metapopulations consist of large source subpopulations surrounded by smaller sink subpopulations where predictable migrations correlate with habitat favorability. From 1996-2003, *Trachemys scripta* were trapped in a permanent pond in central Oklahoma. In 2003, drought resulted in an influx of unmarked adults, presumably immigrants from nearby ephemeral ponds, suggesting a source-sink metapopulation. From 2004-2006, I sampled 14 ponds, and analyzed migration data from 1996-2003 to select among population models. My objectives were to define natural population boundaries, test the source-sink hypothesis, and estimate migration rates and population density. From 1996-2006, 18,285 captures of 2,087 turtles were recorded, including 622 migrants. The direction of migrations supported the source-sink hypothesis. Migrations were negatively correlated with inter-pond distance. Using POPAN, population density estimates from 2005 were 135 individuals/ha, compared to 364 individuals/ha from 2003. These results suggest that long-term population studies should expand sampling to include multiple ponds in order to account for migration.

INTRODUCTION AND LITERATURE REVIEW

A Review of Population Models

Primary goals in many ecological studies are to define the boundaries of natural populations and estimate their densities (Andrewartha and Birch, 1984), both of which are prerequisites for studying life histories (Stearns, 1977), genetics and evolution (Mayr, 1970; Pianka, 1983), conservation (Hanski, 1999; McCullough, 1996), and ecological interactions (Berryman, 1981). A population is a group of individuals of the same species occupying a given area (Wilson and Bossert, 1971). However, under this definition, it is not clear how either the group of individuals or the given area should be defined, leading to multiple interpretations (Camus, 2002). Because defining population boundaries and measuring population densities may be daunting tasks, various models based on mark-recapture methods have been developed.

It is common to use mark-recapture methods to sample animal populations (Greenwood, 1996). The basic premise is to capture a sample of the population, mark the individuals, release them, and obtain subsequent samples. Assuming that the proportion of marked animals in the subsequent samples is the same as that in the whole population, the number of individuals in the population is estimated using the ratio of marked to unmarked individuals in the subsequent samples (Greenwood, 1996). All mark-recapture methods assume that identifying marks are not lost, marks do not affect mortality, and all individuals have an equal chance of capture. Various population models have been developed that differ with respect to assumptions about the level of population closure, which can be tested using mark-recapture methods (Lindeman, 1990). Below, I describe

three models used to define population boundaries and estimate density: closed, open, and metapopulation models.

Closed Population Models

The earliest population models to be developed were closed models (Kendall, 1999; Fig. 1). Closed models assume that a population does not experience additions (births or immigrations) or deletions (deaths or emigrations) for the duration of the study (Greenwood, 1996; Kendall, 1999, Pollock, *et al.*, 1990, White *et al.*, 1982). Closed models are robust and allow for estimations of population density (see below; Schnabel, 1938) when the model assumptions are not violated. During short-term, mark-recapture studies when additions and deletions can be assumed as negligible (Pollock *et al.*, 1990), closed models can be applied to estimate density for populations that are demographically closed (no births/deaths) or geographically isolated (islands, lakes). However, when studies encompass multiple seasons, or when the population is neither demographically nor geographically closed, these models are inappropriate and may yield estimates of population density that are upwardly biased (Greenwood, 1996).

Open Population Models

When permanent additions or deletions of individuals occur during a study, open population models may be appropriate (Greenwood, 1996; Fig. 1). Although open models are more flexible and relax most of the assumptions of closed models (Jolly, 1965; Seber, 1965), they do not allow for round-trip migrations (Amstrup *et al.*, 2006; Pollock *et al.*, 1990). Studies of populations that encompass multiple seasons, are demographically open, or are geographically isolated best fit this model (Hixon *et al.*,

2002). Methods such as Jolly-Seber are commonly used to estimate density (N), and offer other parameter estimates (see below; Jolly, 1965; Seber, 1965).

Metapopulation Models

Most empirical data do not support the assumptions of either closed or open population models (Hanski, 1999). Consequently, contemporary population ecologists have developed metapopulation models to describe the dynamics of animal populations. Replacing island biogeography theory (MacArthur and Wilson, 1963; 1967) as the dominant model for conservation biology, metapopulation models allow for additions, deletions, permanent (*i.e.*, one-way), and round-trip migrations within the population (Hanski and Simberloff, 1997; Fig. 1). As originally proposed by Levins (1970), classical metapopulation models are predicated on the assumptions that multiple patches are identical in area and isolation distance, that all patches are reciprocally linked by migrations (Fig. 2), and that the migration rates and fluctuations in demographics are expected to be equal among subpopulations (McCullough, 1996). In theory, classical metapopulation models are stable, but several assumptions make them very difficult to apply to field studies. Variations of classical metapopulation theory allow for a more realistic application to animal populations by relaxing the assumptions of homogeneity in patch size, isolation distances, and migration rates (Harrison, 1991).

Classical metapopulation models may be manipulated into multiple variations. Two metapopulation variations that may be relevant in my study are patchy and source-sink models (Fig. 2). Patchy metapopulation models address the situation where all individuals migrate among patches. In such models, the patches (subpopulations) are so well mixed and interconnected by migration that they function as a single population

(Fig. 2). Essentially, patchy metapopulations should be viewed as one large spatially discontinuous population (Bowne and Bowers, 2004). Extinctions of subpopulations may occur frequently, but are of short duration resulting from rapid recolonization by individuals immigrating from other subpopulations (Harrison, 1991; Snäll *et al.*, 2003).

By contrast, source-sink metapopulations consist of one large source subpopulation that is impervious to extinction and is surrounded by smaller sink subpopulations that are prone to extinction (Harrison, 1991; Pulliam, 1988; Fig.2). The stable source subpopulation and the unstable sink subpopulations share migrants in a predictable manner. During favorable environmental conditions, the direction of migrations is from the source to the sinks because individuals attempt to exploit new habitat and resources and/or escape from high population densities and competition within the source subpopulation (Harrison, 1991). By contrast, high migration rates from the sinks to the source are expected during unfavorable environmental conditions resulting from insufficient food sources, reproductive failure, and/or habitat instability (Harrison, 1991).

Early methods of estimating metapopulation density assumed a closed metapopulation with open subpopulations, and used basic closed and open methods to estimate densities such as those proposed by Schnabel and Jolly-Seber (see below; Jolly, 1965; Roughgarden and Iwasa, 1986; Schnabel, 1938; Seber, 1965). Estimating metapopulation density has been applied with great success to short-lived organisms such as insects (Schtickzelle *et al.*, 2003; Hanski *et al.*, 2000), small mammals (Lidicker, 1962), and amphibians (Gill, 1978; Trenham, 1998). Application of metapopulation models to longer-lived organisms requires longer-term, mark-recapture studies that

encompass multiple seasons and extends the spatial scale of sample sites to incorporate and measure the possibility of migrations among localized subpopulations (Burke *et al.*, 1995; Elmhagen and Angerbjörn, 2001; Moilanen, 2000).

Selecting the appropriate model

The selection of an appropriate population model can occur after data are collected on five variables that describe migration: occurrence, permanence, connectivity, timing, and direction (Hansson, 1991). The occurrence of migration is whether or not individuals migrate into or out of the area under study. Permanent (one-way) migrations occur when individuals move between populations and do not return, whereas round-trip migrations are when individuals temporarily change subpopulations but eventually return to the original subpopulation. Connectivity between patches is the percentage of individuals that undergo round-trip migrations during the study. The direction of migrations are defined as into or out of the study area, and depend on physical and/or biotic conditions.

After documenting the occurrence of migration and obtaining estimates of permanence, connectivity, timing, and direction, selecting appropriate population models is straightforward (Fig. 3). The occurrence of migration provides an unequivocal test of whether or not closed population models are appropriate. If migrations never occur, then open and metapopulation models are rejected and closed models are appropriate. By contrast, closed models are rejected if migrations occur. Moreover, the permanence of migrations is further used to evaluate the applicability of open or metapopulation models. If all migrations are permanent, open population models apply and permanent migration rates may be estimated. If migrations are round-trip, open population models are rejected

and metapopulation models are appropriate. In this event, connectivity, timing, and direction of migrations are used to select among types of metapopulation models. If all of the individuals in the metapopulation participate in round-trip migrations (connectivity = 100%), then patchy metapopulation models are appropriate (Harrison, 1991). If the connectivity is greater than zero but less than 100%, then alternate metapopulation models, specifically source-sink metapopulation models, should be considered. If the timing and directionality of migrations correspond with movement of individuals away from and toward sinks during unfavorable environmental conditions and favorable conditions, respectively, then use of source-sink metapopulation models is supported.

Estimating Population Density

Closed models allow for estimations of population density (N). They are based on the Schnabel method (1938), and use the following equation (see Table 1 for definition of terms).

$$N_i = \frac{\sum n_i M_i^2}{\sum n_i M_i}$$

For open populations, estimates of densities using Jolly-Seber methods are based on the following equation. They are more complex and may require computational programs such as POPAN (Pollock and Alpizar-Jara, 2005; White and Burnham, 1999), but have the advantage of offering additional estimates of survival (ϕ), capture (p), and recruitment rate (ρ ; see Table 1 for definition of parameters).

$$N_i = \frac{(M_i + 1)(n_i + 1)}{(m_i + 1)}$$

Contemporary methods of estimating population density in metapopulations require the use of computer programs such as MARK (White and Burnham, 1999), and provide parameter estimations (i.e., ϕ , p , $pent$, and N) using mark-recapture data (see Table 1 for definition of parameters). Using bootstrapping methods, these programs estimate confidence intervals, and variance for model parameters using maximum likelihood techniques. Parameters (p , ϕ , and $pent$) may be held constant between sampling encounters or allowed to vary by group (age, sex, size) and/or time effects. Models are created using different combinations of parameters and constraints, and run to derive estimates of population density (N). The most parsimonious model may be selected by comparing Akaike Information Criterion (AICc), AICc weight, model likelihood, and number of parameters (Cooch and White, 2006).

Akaike's Information Criterion (AIC) is a measure of goodness of fit for estimated statistical models (Akaike, 1974) and AICc is a correction for small sample sizes that should be used regardless of sample size (Burnham and Anderson, 2002). AICc weight, model likelihood, and the number of parameters all determine which model is the best fit for the data set. The greater the AICc weight and number of parameters included in the model help to identify the best fit model with the greatest flexibility. As the number of parameters increases, the model fit increases. However, the precision of the individual parameters decreases. Therefore, the model with the lowest AICc is selected to balance model fit and precision (Burnham and Anderson, 2002).

Review of Migration Studies in Freshwater Turtles

Although freshwater species of turtles that inhabit ponds are capable of inter-pond migrations (Gibbons *et al.*, 1990), few population studies have measured occurrence, permanence, connectivity, timing, and direction of turtle migrations in a nested set of ponds. Instead, most studies focus on singular ponds and assume that migrations are negligible. Documented migrations in turtle populations that are geographically isolated (Rose and Manning, 1996), or where droughts are uncommon (Christiansen and Bickham, 1989) are rare. By contrast, migrations occur frequently where ponds are ephemeral (Morales-Verdeja and Vogt, 1997; Buhlmann and Gibbons, 2001), where high levels of intraspecific competition driven by high population density (Hansson, 1991) or intense intrasexual competition driven by skewed sex ratios (Gibbons *et al.*, 1990) are present, and in populations that are fragmented (Cagle, 1944; Bowne *et al.*, 2006; Gibbons, 1970).

The red-eared slider turtle (*Trachemys scripta*) is a semiaquatic freshwater turtle with a broad geographic range extending from the coastal eastern United States to Central America (Ernst *et al.*, 1994). This species is sexually dimorphic (females are larger than males) and a habitat generalist that prefers undisturbed, lentic waters supporting heavy vegetation (Cagle, 1950). *Trachemys scripta* feed and mate underwater but emerge to lay eggs, bask, and migrate (Gibbons, 1990). *Trachemys scripta* occurs in high abundance throughout its geographic range, and are usually the most abundant species in turtle assemblages (Gibbons, 1990; Stone *et al.*, 2005). Red-eared sliders are a good model system for studying population organization because the distribution of individuals is highly fragmented into singular ponds (Gibbons, 1970) among which migrations have

been documented (Bennett *et al.*, 1970; Burke *et al.*, 1995; Cagle, 1944; Cagle, 1950; Gibbons, 1990; Morreale *et al.*, 1984; Parker, 1984; Parker, 1990; Scribner *et al.*, 1986; Stone *et al.*, 2005; Table 2).

Since 1996, P. A. Stone has conducted research on *T. scripta* in a large permanent pond (Pond A, Fig. 4) and two smaller satellite ponds (Ponds B and C, Fig. 4). Round-trip migrations of *T. scripta* between Ponds A and B and Ponds A and C have been documented (Babb, 2004; Stone *et al.*, 2005); for demographic purposes, the three ponds were considered one closed population (Stone *et al.*, 2005). High trapping effort in this system during 1996-2002 revealed unusually high estimates of density (414 individuals/ha, using the Schnabel method; Stone *et al.*, 2005). During a 2003 drought, there was a dramatic increase in capture rates and many new captures of previously unmarked adults in Pond A (P. A. Stone, unpublished data). The influx of unmarked turtles suggested that population boundaries were spatially larger than the individual ponds that were previously sampled. The direction of the migrant influx was positively correlated with the timing of drought, and suggested that a source-sink metapopulation model may apply to this system.

My objectives were to: 1) define the natural population boundaries in this system by collecting data on occurrence, permanence, connectivity, timing, and direction of migrations; 2) test the hypothesis that this system is a source-sink metapopulation; and 3) estimate migration rates and population density using the methods that best fit the ecological parameters that I determined empirically.

METHODS

Study Area

The study area consisted of 14 ponds located near 178th street and Morgan Road in Piedmont, Oklahoma (35° 39' 45" N, 97° 41' 21" W; Fig. 4). The habitat surrounding the ponds was a mosaic of human residences and farms divided into 2.59 km² grids by roads. Grass lawns, pastures, fields, and undeveloped secondary growth were present throughout the study area. The largest and only permanent pond (Pond A) was approximately 1.95 ha in area and 2 m in depth (Stone *et al.*, 2005). *Trachemys scripta* was the most abundant species in the turtle assemblage within this study area, which also included the common snapping turtle (*Chelydra serpentina*), yellow mud turtle (*Kinosternon flavescens*), river cooter (*Pseudemys concinna*), and spiny softshell turtle (*Apalone spinifera*; Stone *et al.*, 2005). Within 3 km of Pond A were 13 smaller ponds (Fig. 4). The satellite ponds varied in size and depth, but all were less than 1.0 ha in area, less than 2 m deep, and were ephemeral (Table 3).

Data Collection

Trapping Methods

Most turtles were captured using hoop nets (0.6 - 1.2 m diameter, 2.5 - 3.8 cm mesh), baited with sardines, and were monitored daily. Captured turtles were identified from previous markings or marked with marginal scute notches, as described in Cagle (1939). In addition to sampling the 14 ponds with hoop nets, turtles were collected from a wire basking trap (Pond K only; Table 4), and two individuals from Pond I were collected after they were killed by the land owner (Table 4).

Turtle Measurements

Pond ID, turtle ID numbers, and recapture status were recorded for all captured turtles. To ensure proper turtle ID numbers, medial plastron length, sex, and any unique features that could verify identification of individuals were also recorded. Immediately after data were recorded, living turtles were released on the shore of the pond where captured.

Trapping Effort

From 2004-2006, turtles were trapped March through October (Cagle, 1950; Gibbons, 1990). Trap effort varied by year. The objective was to sample as many ponds each week that was permissible by land owners and/or drought conditions. In 2005, the objective was to sample each pond once per week. The number of traps per pond depended on pond size, with more traps being set in larger ponds. In 2004, we obtained permission to trap in seven ponds (Table 4). In 2005, we had access to 13 ponds (Pond I salvage only; Table 4). In 2006, drought limited trapping to four ponds (Table 4). In addition, I drove around the entire study site to search for individuals crossing the adjacent roads or that had been killed by traffic. I also walked around the perimeter of each pond to document turtles that were migrating between ponds, and to search for shells of dead turtles. I identified marks from the shells of the dead turtles and deposited them in the Herpetology Division of the University of Central Oklahoma's Collection of Vertebrates. Because my trapping period was relatively short compared to the lifespan of *T. scripta*, I supplemented my data with additional trapping data collected during 1996-2003 (P. A. Stone, unpublished). Combining the 1996-2006 trapping data from Pond A (Table 4) with 2004-2006 trapping data allowed me to identify the number of shared

migrants (both permanent and round-trip) between Pond A and Ponds B-N over a ten-year period.

Pond Measurements

Using a 3-D Geographic Information System (Google Earth), I obtained aerial images and GPS coordinates of the study site. Using the aerial image and the polygon tool, I constructed polygons around each pond and used the area option to calculate the surface area of each pond. I then estimated the midpoints of each polygon (pond) so that I could connect the polygons with straight lines and used the distance tool to estimate isolation distance among ponds to the nearest meter. Finally, I constructed a map of the study site by cropping and labeling the aerial image (Fig. 4).

Drought History

In 2003, there was a drought that extended until 22 May 2004, resulting in complete drying of most satellite ponds (Table 3). This presumably forced all of the resident *T. scripta* in the satellite ponds to emigrate. After 22 May 2004 and throughout the 2005 trapping season (*i.e.*, 2 Mar – 27 Oct), rainfall filled the ponds, presumably allowing individuals to return to the satellite ponds. In 2006, drought again completely dried most satellite ponds. Because the study period included an exceptionally wet period (2005) bracketed by periods of profound drought (2003, 2006), I could test the hypothesis that a source-sink metapopulation model best described the study site. If migration varied in response to pond water levels, it should have been apparent within these study years. In 2005, when the ponds were full, I estimated water depth by wading out to the deepest point, placing a wooden stake at the top of the silt, and then measuring the depth with meter tape. Drought history was determined by comparing notes

describing water depth from field data (1996-2005; P. A. Stone), visual estimates of water levels by the land owners (2004), and personally estimating water levels (2005-2006; Table 3).

Defining Population Boundaries

To define the population boundaries, I analyzed occurrence, permanence, connectivity, timing, and direction of migrations to follow the flowchart in Figure 3 and selected among closed, open, and metapopulation models. I defined migrants as individuals captured between 1996 and 2006 in two or more ponds.

Testing the Source-Sink Metapopulation Hypothesis

Using the predictions of source-sink metapopulation models (Fig. 2), I used a sign test to test if migrations were random or had directionality. In my study system, Pond A was the most likely source pond and the satellite ponds were likely sink ponds. Significant directionality of migrations away from the sinks during drought and away from the source during wet periods was expected of the source-sink metapopulation hypothesis (Fig. 3).

For the defined population, I pooled all round-trip migrants from 2003, 2005, and 2006. Because fluctuating pond water levels made it difficult to define migration direction in 2004, I excluded this year. Round-trip migrants were defined as individuals that emigrated out of a population and later returned. However, two other types of round-trip migrants were apparent; those that migrated multiple times between two ponds during one season, and those that migrated among multiple satellite ponds before returning to Pond A. Because of the difference in pond water levels, individuals that

migrated in 2003 or 2006 were predicted to migrate from sink to source whereas individuals that migrated in 2005 were predicted to migrate from source to sink. Migrants were sorted according to their emigration direction: from the source or from the sink. To avoid replication of individuals, I excluded individuals that engaged in multiple round-trips and tested each direction separately. Using a sign test (Zar, 1999), I tested the null hypothesis of no difference in the direction of emigration by year.

Estimating Migration Rates

I estimated the migration rate from each satellite pond to Pond A. Migration rates were determined by dividing the number of shared migrants between two ponds by the total number of individuals captured in both ponds. Using a Spearman's rank correlation test, I tested if there was a correlation between pond isolation distance and migration rate.

Estimating Population Density

Once the appropriate population boundaries were established, population density was estimated using POPAN in the computer program MARK (White and Burnham, 1999). Using mark-recapture data, from March through October 2005, when all 14 ponds were intensively sampled (Table 4), I pooled capture data by month (eight sampling occasions) to ensure large sample sizes and increase the accuracy of my estimate. The mark-recapture data for all individuals were then entered into an input file format accepted by the computer program MARK.

The best fit model was selected by comparing AICc weight, number of parameters, and model likelihood from all possible models. Each parameter (p , ϕ , p_{ent}) had a time constraint and was either held constant or allowed to vary between months. No group or individual effects were analyzed. Models varied from fully time dependent

$(p\{t\}phi\{t\}pent\{t\})$ to fully time independent $(p\{.\}phi\{.\}pent\{.\})$; Table 6). The presence of a (t) or $(.)$ after a parameter meant that the model was structured so that the estimate for that parameter was time specific or constant each month, respectively.

Before models were run through POPAN, additional parameter constraints were necessary to avoid convergence error (Cooch and White, 2006). I specified the Link Functions as Parameter Specific, allowing me to specify different constraints to each parameter in contrast to using the default link. Because the parameters were probabilities (Table 1), I constrained p , phi , and $pent$ from zero to one (specified Sin link for p and phi and MLogit link for $pent$). The population density estimate (N) was not constrained from zero to one (specified Log link). Running this corrected model through POPAN and selecting Derived Estimates provided N for the defined population with a 95% confidence interval (Cooch and White, 2006).

RESULTS

There were 5,796 captures of 1,293 red-eared sliders during 2004-2006. During 1996-2006, 18,285 captures of 2,087 turtles were recorded. There were 1,826 individuals captured in Pond A and 883 individuals in the satellite ponds (Table 5). There were 460 individuals that were not recaptured after they were marked and 72 individuals were recovered dead. Of 1,627 recaptured individuals (78%), 622 (38%) individuals migrated between Pond A and the satellite ponds. Thirty-four percent of all individuals captured in Pond A were also captured in a satellite pond, whereas 70% of all individuals captured in a satellite pond were also captured in Pond A. Within the entire study site, 1,187 males were trapped compared to 705 females (sex ratio: 1.7:1). Of these males, 345 migrated (29%), compared with 301 female migrants (43%). Of the 195 marked juveniles, only 21 migrated (10%). Of the six individuals that migrated the farthest distances (Pond A to N, M; 1520-1700 m) two were male, two were female, and two were juveniles.

Defining Population Boundaries

I rejected closed population models because there was at least one permanent migrant between Pond A and each of the 13 satellite ponds (Table 5). Seven of 13 satellite ponds (Ponds B-G and L) shared at least one round-trip migrant with Pond A (Table 5), rejecting open models. Therefore, these 7 satellite ponds surrounding the large pond (Ponds A-G and L) were best described as a metapopulation. The remaining 6 satellite ponds (ponds H-K and M-N) shared only permanent migrants with Pond A and were best described as open populations (Fig. 5).

Connectivity

To determine which metapopulation model was appropriate, I analyzed the connectivity between each satellite pond and Pond A. I rejected patchy population models because all ponds (B-G, L) had a connectivity greater than zero and less than 100% (1.8-59.3%; Table 5); connectivity decreased as distance from Pond A increased (Spearman's rank correlation, $Rho = -0.929$, $p < 0.1$). Of the 273 round-trip migrants, 50 individuals engaged in multiple round-trips between ponds. For example, based upon 282 captures from 1996-2006, one turtle completed seven round-trip migrations between ponds A and B (220 m) with the quickest taking only three days. Forty-four turtles made round-trip migrations that included stops at multiple combinations of ponds before returning to Pond A. For example, one turtle made nine migrations within the defined metapopulation that included stops at ponds B, C, D, and E before returning to Pond A (Fig. 6). Yet another turtle migrated between ponds A and B and then traveled outside the defined metapopulation boundaries to Pond H (880 m) before returning to Pond A (Fig. 7).

Testing the Source-Sink Metapopulation Hypothesis

In 2003 and 2006 when the majority of the satellite ponds were dry, there was significant directionality (sign test, $p < 0.001$; Table 6) of migrations from sinks to source. By contrast, in 2005 when the majority of the satellite ponds were filled with water, there was significant directionality (sign test, $p < 0.001$; Table 6) of migrations from the source to sinks.

Migration Rates

Migration rates from the satellite ponds were negatively correlated (Spearman's rank correlation, $Rho = -0.933$, $p < 0.01$) with distance from Pond A (Figs. 8 and 9). Migration rates from the two satellite ponds closest to Pond A (<320 m) were above 90%, whereas migration rates from the satellite pond farthest from Pond A (>1700 m) were near 4%. Migration rates ranged from 74-98% when ponds were less than 690 m in distance from Pond A and dropped below 25% when pond distance exceeded 920 m (Table 5). The greatest straight-line migration was 1.7 km (Pond A to N; Table 5). Within the defined metapopulation, migration rates from the sink ponds to the source pond was negatively correlated (Spearman's rank correlation, $Rho = -0.929$, $p < 0.1$) with inter-pond distance.

Population Density

All possible combinations of parameters (p , ϕ , $pent$) and time effects (t , .) yielded eight possible models (Table 7). I chose the best fit model, $p(t)\phi(t)pent(t)$, where capture probability (p), survival (ϕ), and probability of entrance ($pent$) were time dependent (AICc = 3314.3, AICc weight = 0.9943, model likelihood = 1.0000, parameters = 20; Table 7). According to the AICc weights, the best fit model had 99 times more support than the next best model (weight₁ = 0.9943, weight₂ = 0.0057; Table 7). Within the defined 6.54 ha metapopulation of ponds A-G and L, the metapopulation density estimates from POPAN in 2005 were 885.7 ± 19.5 individuals (135 individuals/ha). In 2003, 899 individuals were captured in Ponds A-C with a collective pond surface area of approximately 2.48 ha and a metapopulation density estimate of

362.5 individuals/ha. In 2005, 845 individuals were captured in Ponds A-N with a collective pond surface area of 6.54 ha and a metapopulation density estimate of 129 individuals/ha.

DISCUSSION

Defining Population Boundaries

The population model that best described this study system is a source-sink metapopulation (ponds A-G and L) surrounded by several open populations (ponds H-K, M-N). Because all ponds shared at least one migrant and because neighboring ponds outside of the study area were not sampled, there is a possibility that the metapopulation boundaries were underestimated. Because my study was short relative to the lifespan of *T. scripta*, I may not have detected round-trip migrations among Pond A and open populations that occur at a low frequency. When analyzing individuals that migrated among multiple satellite ponds before returning to Pond A (44 individuals; Fig. 7), the defined boundaries of the metapopulation were questioned. Using my definition, the metapopulation of ponds A-G, and L was determined by the presence of migrants that completed round-trip migrations between Pond A and nearby satellite ponds. However, some individuals migrated from satellite pond to satellite pond before returning to Pond A. If I include these “stepping stone” satellite ponds, such as Pond H in Figure 7, the metapopulation would expand to incorporate two more ponds, H and J (Fig. 5).

As the length of the study and the number of ponds sampled increased, so did the number of round-trip migrants. In a 26 year metapopulation study of *T. scripta* by Burke *et al.* (1995), there was a significant effect of study duration on the metapopulation boundaries. Burke *et al.* (1995) reported that five years after the first individuals in the population were marked, the metapopulation boundaries increased (69 ha to 841 ha), and after ten years, only four of the nine subpopulations had been identified. This suggested that the metapopulation boundaries of ponds A-G and L that I accepted should be

considered as a minimum estimate. The open populations surrounding the metapopulation may potentially be part of the defined metapopulation or may be part of a neighboring metapopulation. Outside of the study site, approximately three km east of Pond A, is a large, permanent pond (Fig. 10). The surrounding open populations (ponds M and N, specifically) may be used as stepping stones by permanent migrants to connect two metapopulations (Fig. 10). Population boundaries and even the geographic range of this species may be limited by the presence of permanent source ponds.

Migration distances (220-1700 m) were comparable with those of other studies on this species (Bowne *et al.*, 2006; Morreale *et al.*, 1984; Thomas and Parker, 2000; Table 2), and migration rates within my metapopulation were negatively correlated with pond isolation distance (Fig. 9), similar to results from other freshwater turtle populations (Carter *et al.*, 2000; Thomas and Parker, 2000; Morreale *et al.*, 1984). Thomas and Parker (2000), observed 173 individuals migrating within a metapopulation of red-eared sliders. Over 93% of the individuals migrated short interpond distances (15-150 m) compared to 6 % that migrated to ponds at the edge at the study site (1200 m). Similarly, in a study of bog turtles (*Clemmys muhlenbergii*), the migrations appeared to decrease as distance increased (Carter *et al.*, 2000).

Connectivity among the source-sink metapopulation of ponds A-G and L was also negatively correlated with pond isolation distance. Therefore, round-trip migration rate decreased as sink pond distance from the source pond increased. In a metapopulation of painted turtles (*Chrysemys picta*), pond connectivity decreased as distance increased from the closest permanent ponds (Bowne *et al.*, 2006). However, pond water levels were

inferred as a more important factor on connectivity than pond isolation distance (Bowne *et al.*, 2006).

As the satellite ponds were filling with water, the direction of migration was from the source pond to the sink ponds where water was becoming available. Few studies have documented migration during times of abundant rainfall (Parker, 1984) or the return of individuals to an ephemeral pond as water levels increased (Bowne *et al.*, 2006; Buhlmann and Gibbons, 2001; Cagle, 1944; Gibbons *et al.*, 1983; Rose and Manning, 1996; Sexton, 1950). Cagle (1944) recorded individuals of various freshwater turtle species returning to a drained lake after heavy rainfall raised water levels. Although data regarding migrations from source to sink during times of abundant rainfall is sparse, such movements are hypothesized to function as escape from the source pond's high population density and the competition for resources (Gibbons, 1990).

The findings in my study revealed that as the majority of the satellite ponds were drying, the direction of migration was from sinks to source. Migrations resulting from decreasing water levels have been documented in various species of freshwater turtles (Aresco, 2005; Bowne and Bowers, 2004; Buhlman and Gibbons, 2001; Cagle 1944; Cash and Holberton, 2005; Gibbons and Greene, 1978). In a study of painted turtles (*Chrysemys picta*), 46% of marked individuals migrated during normal water levels, compared to 61% that migrated during drought (Bowne *et al.*, 2006). The permanent focal pond in the Bowne *et al.* (2006) study shared no migrants with surrounding ponds during average seasons. However, when drought reduced water levels in the ephemeral ponds, the focal pond received an influx of immigrants. In addition, Christiansen and Bickham (1989) observed mass influxes of unmarked individuals into permanent ponds

during prolonged drought. Directionality of migrations during drought has been documented. In a study by Gibbons *et al.* (1983), 52% of the migrants departing from a drying pond headed toward the closest permanent body of water. The hypothesized function of migrations was to escape unfavorable environmental conditions and exploit the permanent pond for resources where the water levels were not seriously desiccated (Harrison, 1991).

Though my data indicate that migration direction is influenced by pond water levels, there were 50 individuals that migrated between source and sinks, regardless of water levels (Fig. 6). Buhlmann and Gibbons (2001) observed individuals of *Trachemys* and *Chrysemys* migrating into and out of an ephemeral pond when water levels were rising in the spring or drying because of drought, respectively. The migrations of individuals were hypothesized to function as mate searching. Individuals in my study that migrated regardless of water levels may have moved from pond to pond in response to factors that were not analyzed such as mate searching (Buhlmann and Gibbons, 2001; Cagle, 1944; Morreale *et al.*, 1984; Parker, 1984), or preference to patch size, and/or patch shape (Bowne *et al.*, 2006; Brooks, 2003; Goodwin, 2003; Trenham, 1998).

The results of my study suggest that inter-pond migrations were limited by pond isolation distance and the directions of the migrations were dependant on pond water levels. As pond water levels decreased, individuals migrated from smaller sink ponds to stable, permanent source ponds resulting in individuals and subpopulations dependant on source ponds for persistence. For conservation efforts, this concept is essential for protecting the species' entire habitat and migration routes (Aresco, 2005; Bowne *et al.*,

2006; Buhmann and Gibbons, 2001; Hanski and Simberloff, 1997; Steen and Gibbs, 2004).

Population Density

The model with the most support ($p\{t\}phi\{t\}pent\{t\}$) described the study population's capture probability (p), survival (phi), and probability of entrance ($pent$) as time dependent. Because the mark-recapture data were pooled to increase the sample size and the accuracy of the population density estimate, the model parameters varied by month. A more biological-meaningful interpretation would be that the model parameters varied seasonally, as described by Morreale *et al.* (1984). In a population of *T. scripta*, activity and migration patterns varied seasonally resulting from differential reproductive strategies. Males were more active during breeding seasons, whereas females were more active during nesting seasons. Seasonal variation in activity would affect encounter (p), survival (phi), and immigration rate ($pent$).

Population density is a function of population size and available habitat area. Population size fluctuated with additions and deletions of individuals and habitat area fluctuated as a function of pond water levels. The number of individuals captured in 2003 and 2005 fell within or close to the metapopulation density range of 885.7 ± 19.5 individuals as estimated using POPAN. The narrow confidence intervals and the number of individuals trapped supported the population density estimate, and suggested that we sampled the entire metapopulation in both years and supports the selected model. During the drought in 2003, the amount of available habitat (2.48 ha) was much smaller than in 2005 (6.54 ha), but the number of captured individuals was comparable (899 and 845,

respectively). In theoretical source-sink metapopulations, density estimates fluctuate significantly as a function of the amount of available habitat (Hansson, 1991; Hanski, 1999; Hanski *et al.*, 2000; Snäll *et al.*, 2003) and high connectivity between two subpopulations is predicted to affect dynamics such as population density (Parker, 1990), sex-ratio (Doody *et al.*, 2002; Tuberville *et al.*, 1996), and mortality (Aresco, 2005; Steen and Gibbs, 2004).

The source-sink metapopulation was defined by analyzing several years of mark-recapture data that incorporated variable seasons with fluctuating water levels. Accurate population density estimates resulted from defining the natural population boundaries and applying appropriate models. Many studies of long-lived turtle populations limit sampling to singular ponds or seasons potentially underestimating natural population boundaries. For conservation efforts, these results could be detrimental to the adequate protection of an endangered species (Bowne *et al.*, 2006; McCollough, 1996).

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Table 1. Model notations for population density estimation using Schnabel and Jolly-Seber methods.

Statistics	
N_i	total number of animals in the population during the i -th sample
M_i	number of marked animals in the population during the i -th sample
R_i	number of animals already marked when caught in sample i
n_i	number of animals in the i th sample
m_i	number of marked animals in the i th sample
Parameters	
p_i	the capture probability for all animals during the i -th sample
ϕ_i	the survival probability for all animals between the i -th and $(i+1)$ th samples
$pent_i$	the total number of new animals entering the population between the i -th and $(i+1)$ th samples and still in the population at the time $(i + 1)$ th sample is collected
Functions of Parameters	
Schnabel	$N_i = \frac{\sum n_i M^2}{\sum m_i M_i}$
Jolly Seber	$N_i = \frac{(M_i + 1)(n_i + 1)}{(m_i + 1)}$
	$p_i = \frac{m_i}{M_i} = \frac{n_i}{N_i}$
	$\phi_i = \frac{M_{i+1}}{m_i - M_i + R_i}$
	$pent_i = ni + 1 = \phi_i(N_i - ni) + R_i$

Table 2. Published migration distances for red-eared slider turtles, *Trachemys scripta*.

Source	Distance (m)
Bowne <i>et al.</i> (2006)	230-1220
Gibbons (1990)	200-9000
Morreale <i>et al.</i> (1984)	3000-5000
Thomas and Parker (2000)	15-1200

Table 3. Study pond data from 1996-2006. Pond A is the largest and only permanent pond. Ponds B-N are smaller satellite ponds. Isolation distance, pond measurements and impact of drought are provided. Drought levels were determined by comparing notes describing water depth from field data (1996-2005), visual estimates of water levels by the land owners (2004), and personally estimating water levels (2005-2006).

Pond	Distance to Pond A (m)	Perimeter (m)	Area (ha)	Depth (m)	Impact of Drought
A	-	973	1.95	2	Reduced
B	220	176	0.16	0.9	dry
C	320	288	0.37	0.9	reduced
D	520	608	0.86	0.9	dry
E	550	640	0.9	1.3	dry
F	690	369	0.44	0.9	dry
G	730	325	0.3	0.9	dry
H	880	529	0.64	1.1	dry
I	900	-	-	-	?
J	920	189	0.21	1.5	reduced
K	960	156	0.09	1.8	dry
L	1090	273	0.28	1.8	dry
M	1520	232	0.25	1	reduced
N	1700	151	0.09	0.9	dry

Table 4. Trapping history of study ponds. The number traps set in each pond (trap days) and the number of days that traps were set (days trapped) were recorded for each season. Perimeter refers to the number of times that a member of the field crew walked around the ponds searching for red-eared slider turtles (*Trachemys scripta*).

Year	Pond	Trap Days	Days Trapped	Perimeter	Trapping Season	Comments
1996	A	10	2	0	14 Jul - 25 Aug	
1997	A	106	27	0	5 Apr - 19 Sept	
1998	A	292	70	0	17 May - 30 Sept	
1999	A	235	94	0	28 Apr - 10 Sept	
2000	A	177	50	0	8 May - 13 Oct	
	B	2	1	0	15 Jun - 15 Jun	
2001	A	552	100	0	2 Apr - 11 Nov	
	B	20	4	0	24 May - 22 June	
2002	A	1655	195	0	6 Mar - 31 Oct	
	B	31	14	0	17 May - 2 Aug	
	C	31	14	0	15 May - 29 Aug	
2003	A	1291	144	0	9 Mar - 30 Oct	
	B	6	3	0	25 Mar - 27 Mar	
	C	39	20	0	28 Apr - 8 Jul	
2004	A	732	130	0	2 Mar - 29 Oct	
	B	46	27	0	14 Apr - 15 Sep	
	J	2	1	2	17 Sep - 17 Sep	
	K	5	5	2	28 Jul - 12 Nov	Basking net only
	L	29	9	2	3 Aug - 1 Oct	
	M	17	6	2	20 Aug - 11 Sep	
	N	17	7	2	20 Aug - 23 Sep	
2005	A	730	141	9	2 Mar - 27 Oct	Monitored by mowing
	B	37	20	2	7 Apr - 28 Sep	
	C	2	2	2	9 Apr - 22 Apr	
	D	211	82	4	31 Mar - 5 Oct	
	E	213	83	7	2 Apr - 5 Oct	
	F	78	38	3	12 Apr - 5 Oct	
	G	73	42	2	4 Apr - 5 Oct	
	H	104	39	3	7 Apr - 19 Oct	
	I	0	0	0	31 Mar - 31 Mar	Collected through salvage
	J	76	23	2	8 Apr - 25 Sep	
	K	2	2	2	28 Mar - 25 Sep	Basking net only
	L	84	40	3	4 Apr - 28 Sep	
	M	95	45	3	4 Apr - 17 Oct	
	N	82	42	2	4 Apr - 17 Oct	
2006	A	406	74	2	7 Mar - 1 Nov	
	D	20	11	2	15 Mar - 19 Jul	Drought limited trapping
	E	14	11	2	15 Mar - 22 Jul	Drought limited trapping
	F	3	3	2	9 May - 11 May	Drought limited trapping

Table 5. Migration data from 1996-2006. Total number of individuals captured, number of shared, permanent, and round-trip migrants between each satellite pond and Pond A are listed, as are the migration rates (shared migrants/total individuals) and connectivity (round-trip migrants/total individuals). Shared migrants are individuals captured in a satellite pond (B-N) and Pond A.

Pond	Individuals Captured	Shared Migrants	Migration Rate	Permanent Migrants	Round-trip Migrants	Connectivity
A	1826	-	-	-	-	-
B	151	138	0.91	57	81	53.60%
C	54	53	0.98	21	32	59.30%
D	211	161	0.76	151	10	4.70%
E	296	238	0.8	208	30	10.10%
F	34	25	0.74	21	4	11.80%
G	16	3	0.19	2	1	6.30%
H	51	15	0.29	15	0	-
I	2	1	0.5	1	0	-
J	12	3	0.25	3	0	-
K	52	10	0.19	10	0	-
L	56	8	0.13	7	1	1.80%
M	58	1	0.02	1	0	-
N	25	1	0.04	1	0	-

Table 6. Sign test results. Significant directionality was analyzed by a sign test. Round-trip migrants were sorted based on if migration patterns of red-eared slider turtles (*Trachemys scripta*) in 2003, 2005, and 2006 followed the predictions of the source-sink metapopulation hypothesis. In 2003 and 2006 when the majority of the satellite ponds were dry, there was significant directionality of migrations from sinks to source. By contrast, in 2005 when the majority of the satellite ponds were filled with water, there was significant directionality of migrations from the source to sinks.

Direction	Migrated in predicted direction	Did not migrate in predicted direction	Significance
Sink to Source			
(2003, 2006)	78	14	$p < 0.001$
Source to Sink			
(2005)	89	3	$p < 0.001$

Table 7. Model comparisons of Akaike Information Criterion (AICc), AICc weights, model likelihood, and number of parameters as calculated by the computer program MARK. Recapture rate (p), survivability (ϕ), and probability of entrance ($pent$) were constrained according to time independence (.) or time dependence (t). The model with the most support in bold was $p\{t\}\phi\{t\}pent\{t\}$. Numerical convergence was never reached for model number 8, resulting in an error.

Model	Explanation	AICc	AICc Weight	Model Likelihood	Number of Parameters
$p(t)\phi(t)pent(t)$	Encounter rate, survival, and probability of entrance are time dependent	3314.3	0.9943	1.0000	20
$p(t)\phi(.)pent(t)$	Encounter rate and probability of entrance are time dependent; survival is constant	3324.6	0.0057	0.0057	15
$p(.)\phi(t)pent(t)$	Encounter rate is constant; survival and probability of entrance are time dependent	3337.5	0.0000	0.0000	15
$p(.)\phi(.)pent(t)$	Encounter rate and survival are constant over time; probability of entrance is time dependent	3565.6	0.0000	0.0000	7
$p(.)\phi(t)pent(.)$	Encounter rate and probability of entrance are constant over time; survival is time dependent	14979.4	0.0000	0.0000	9
$p(.)\phi(.)pent(.)$	Encounter rate, survival, and probability of entrance are constant over time	15784.5	0.0000	0.0000	2
$p(t)\phi(.)pent(.)$	Encounter rate is time dependent; survival and probability of entrance are constant over time	158510.8	0.0000	0.0000	9
$p(t)\phi(t)pent(.)$	Encounter rate and survival are time dependent; probability of entrance is constant	ERROR			

Table 8. Population density estimates. During drought in 2003, 899 individuals were captured in Ponds A-C with a collective pond surface area of approximately 2.48 ha and a metapopulation density estimate of 362.5 individuals/ha. When all ponds were full in 2005, 845 individuals were captured in Ponds A-N with a collective pond surface area of 6.54 ha and a metapopulation density estimate of 129 individuals/ha.

Year	2003	2005
Number of Individuals	899	845
Pond Area (ha)	2.48	6.54
Population Density (ind/ha)	362.5	129

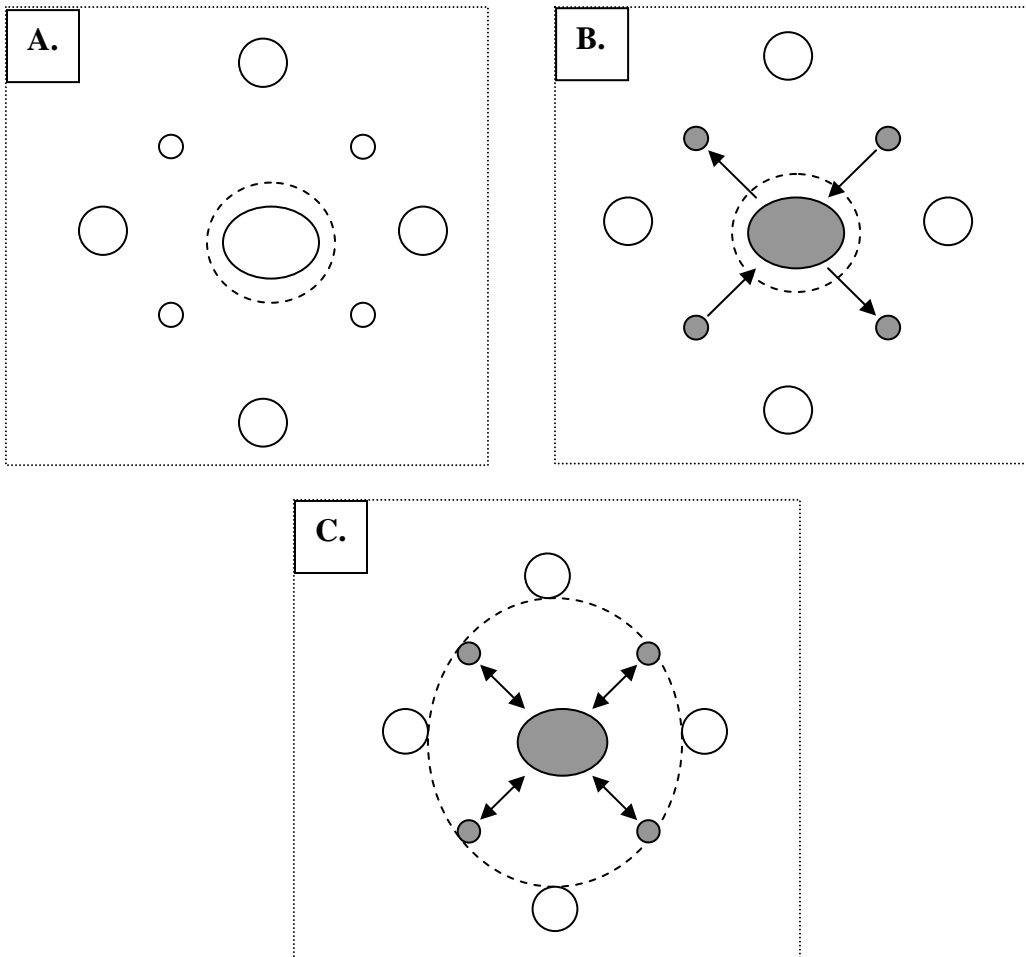


Figure 1. Schematic representation of closed (A), open (B), and metapopulation models (C). The center oval represents the focal population surrounded by other patches of suitable habitat. The sizes of the ovals represent differences in patch size. Shaded ovals represent habitats with shared migrants. The dashed lines illustrate the defined population boundaries. Arrows indicate direction of migration. When the focal population shares no migrants with other patches of suitable habitat, the closed model applies. When, the focal population shares permanent migrants with adjunct patches, the open model is supported. Sharing of round-trip migrants among patches is consistent with the metapopulation model.

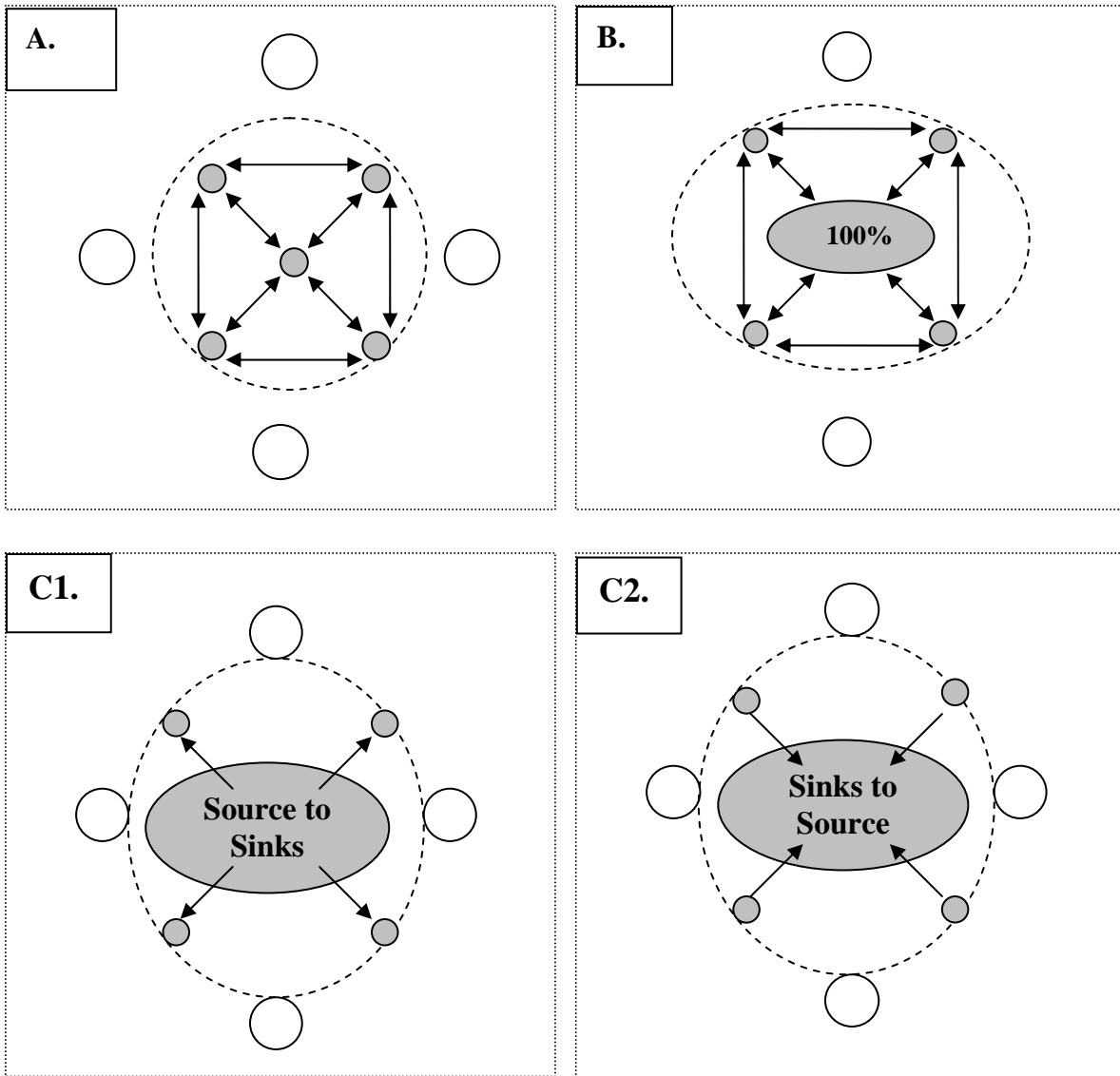


Figure 2. Four variations of metapopulation models. Shading illustrates migrations and relative sizes of circles indicate habitat area. The dashed lines illustrate the defined population. Arrows indicate migration direction. Panel A shows a classical metapopulation where all patches are identical in size, inter-patch distance, and have similar migration rates. Panel B illustrates a patchy metapopulation where all individuals occupy all patches. Panels C1 and C2 illustrate source-sink metapopulations. Panel C1 shows the predicted direction of migration during favorable environmental conditions. Panel C2 shows the predicted direction of migration during unfavorable environmental conditions.

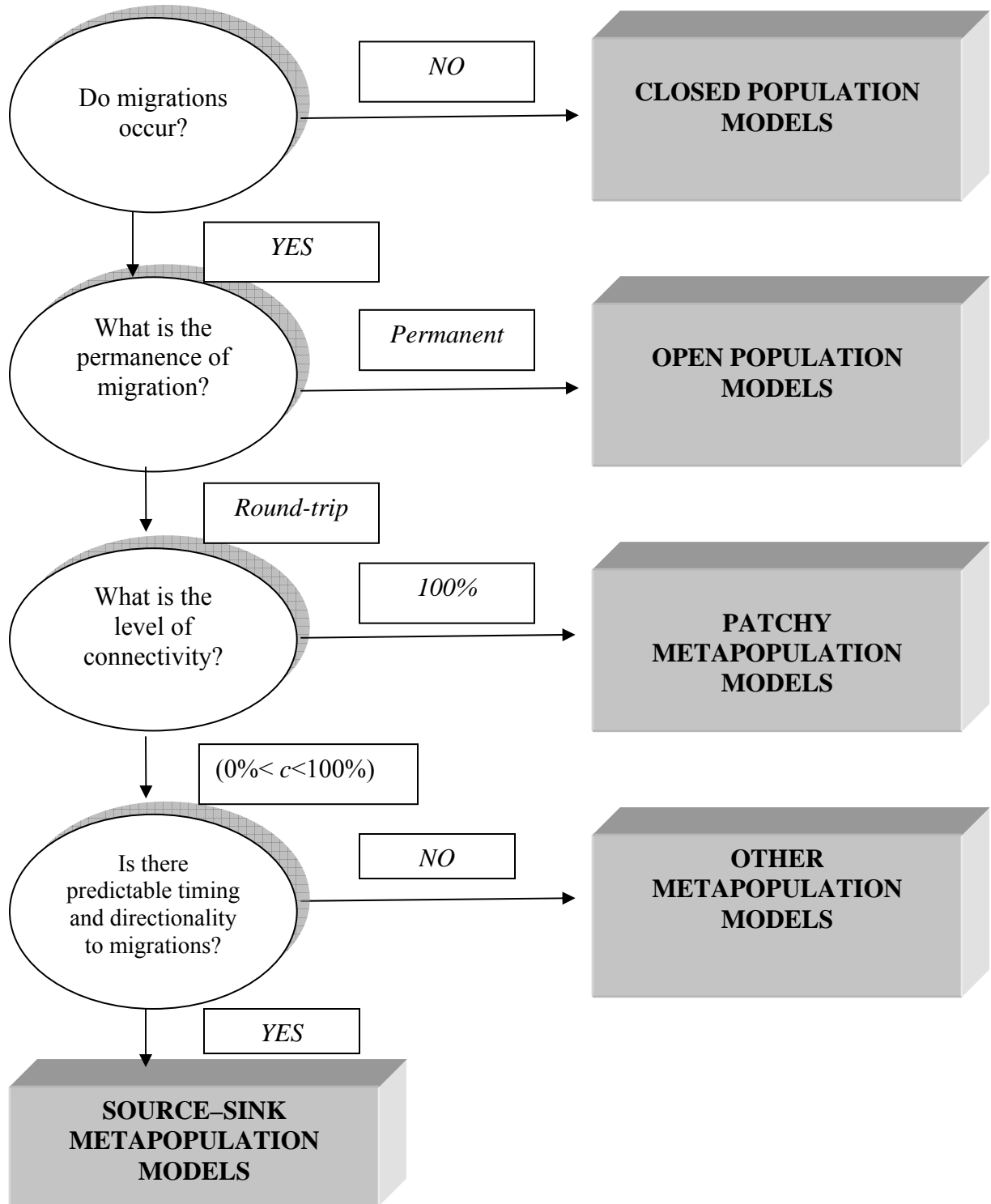


Figure 3. Flow chart outlining methods for choosing the appropriate population model and hypothesis testing incorporating occurrence, permanence, level of connectivity (c), timing, and direction of migrations.

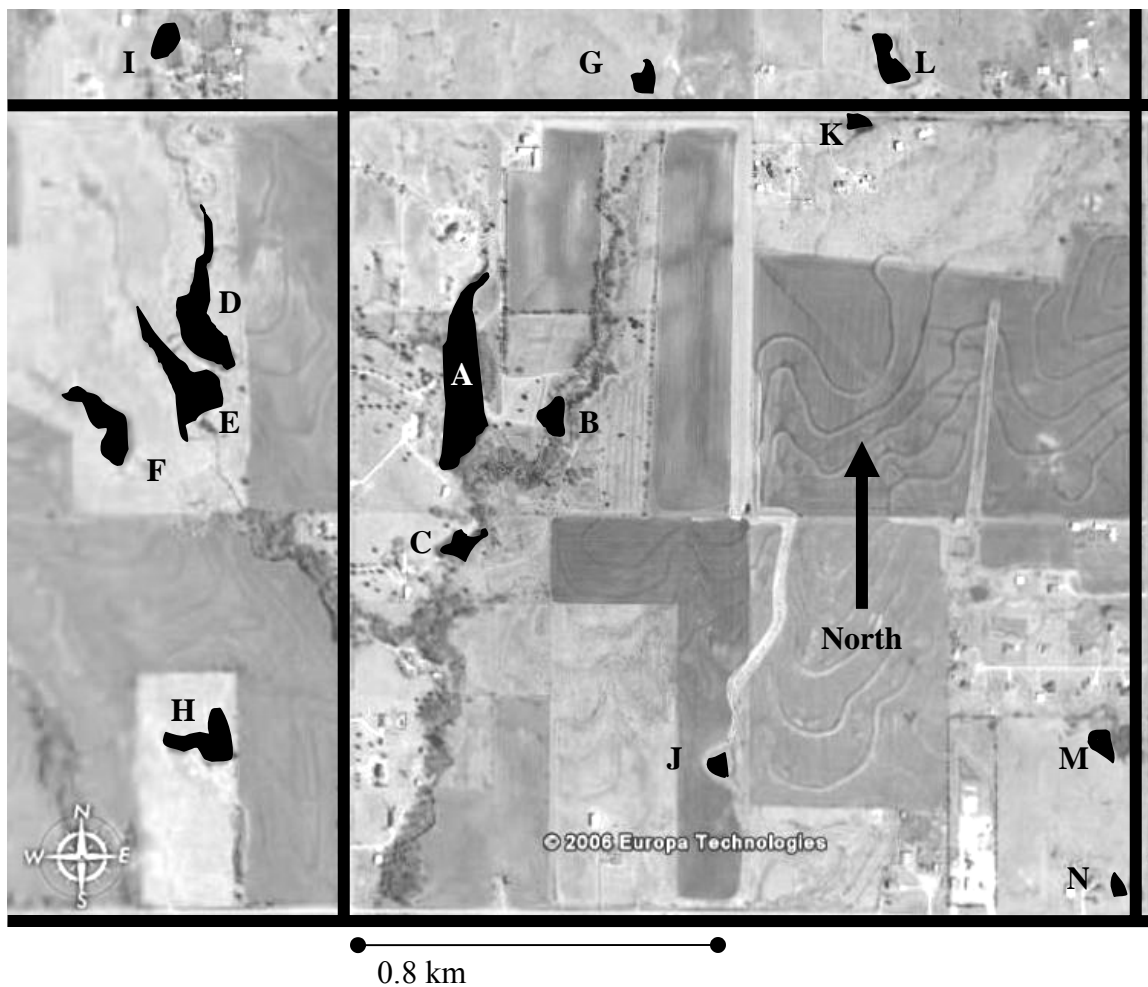


Figure 4. Enhanced aerial image of the study area. The large permanent pond (A) is surrounded by the thirteen smaller satellite ponds (B-N). The solid lines are two-lane country roads. (Obtained from Google Earth: www.GoogleEarth.com)

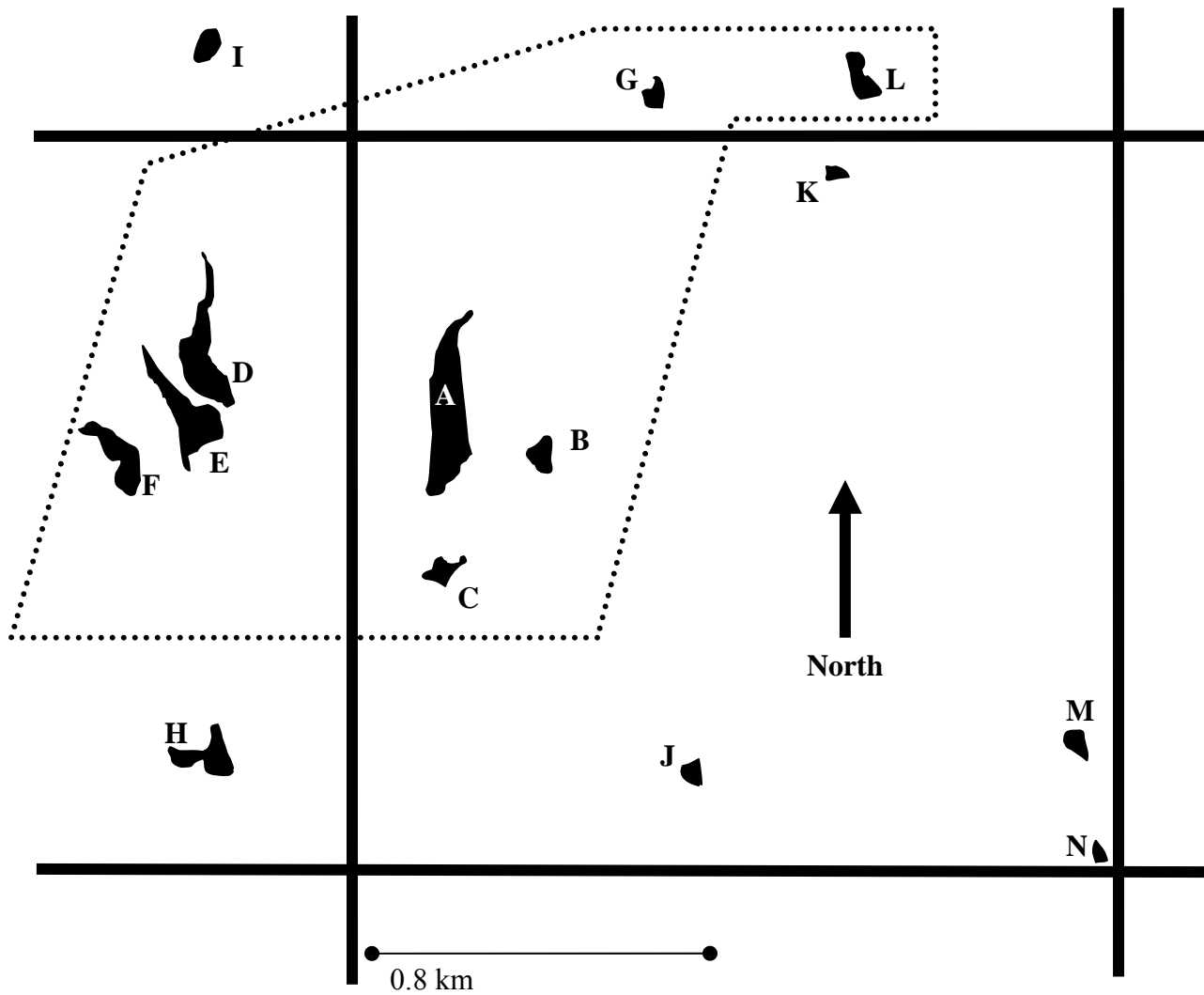


Figure 5. Map of the metapopulation. Dotted line illustrates the defined source-sink metapopulation boundaries.

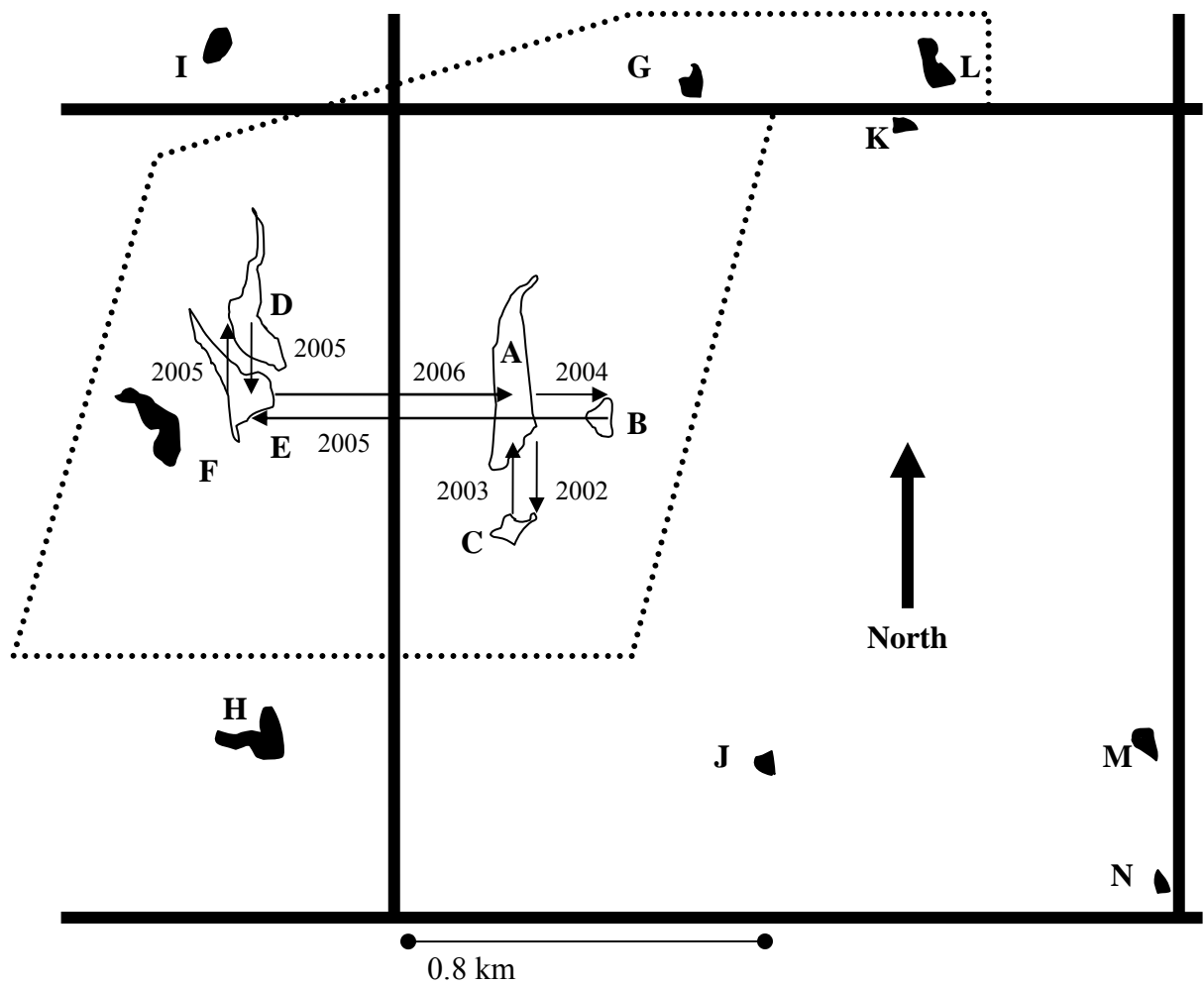


Figure 6. Migration pattern of turtle marked 1622, showing the incorporation of multiple ponds into its home range. The years denote when the individual was captured in a pond differing from that of a previous capture.

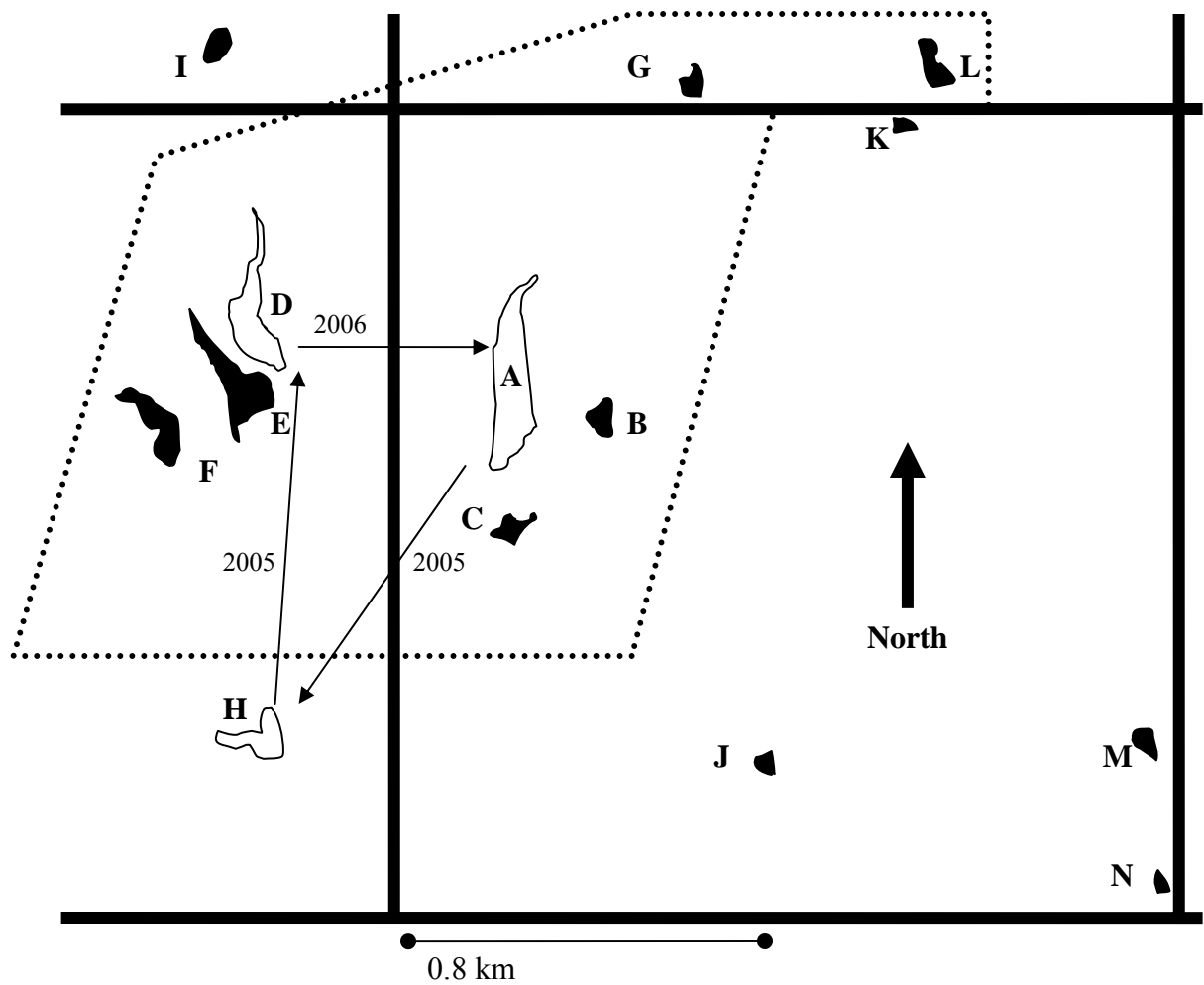


Figure 7. Migration pattern of turtle marked 120, showing the incorporation of multiple ponds both within and outside the metapopulation into its home range. Pond H is outside the metapopulation because there were only permanent migrations between ponds A and H. The years denote when the individual was captured in a pond differing from that of a previous capture.

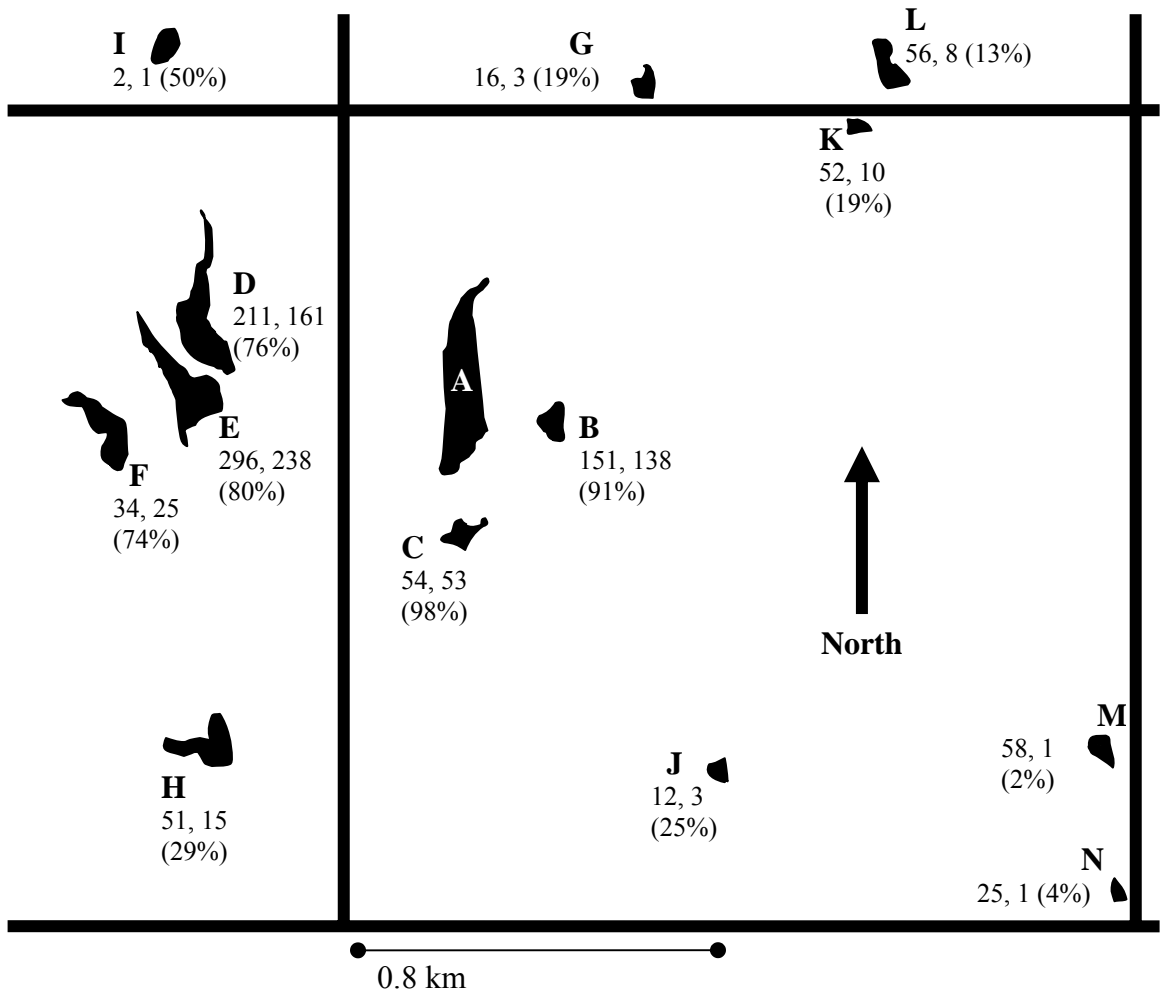


Figure 8. Total individuals, shared migrants, and migration rates for each satellite pond. The first number denotes total individuals captured in each satellite pond. The second number denotes shared migrants between the satellite pond and Pond A. The percentage is the migration rate from the satellite pond to Pond A.

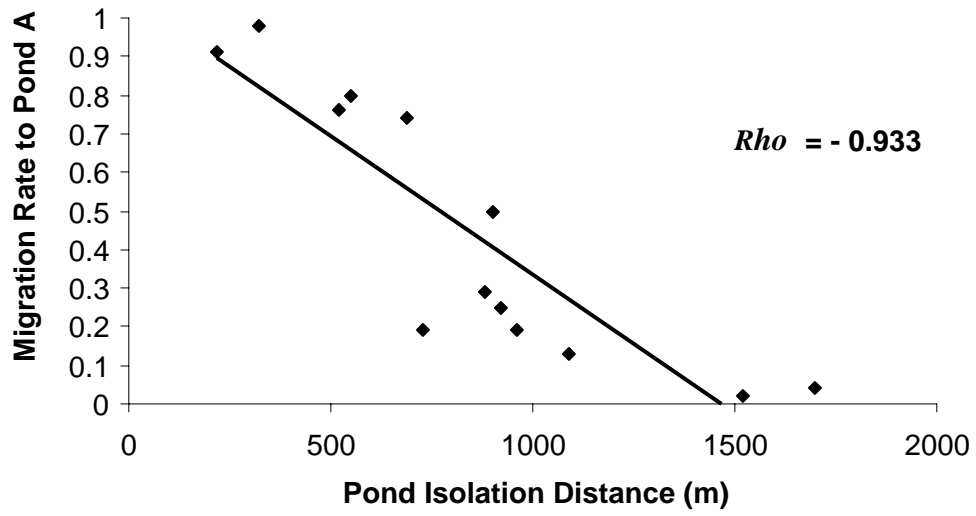


Figure 9. Migration rates from each satellite pond to Pond A in relation to satellite pond distance from Pond A.

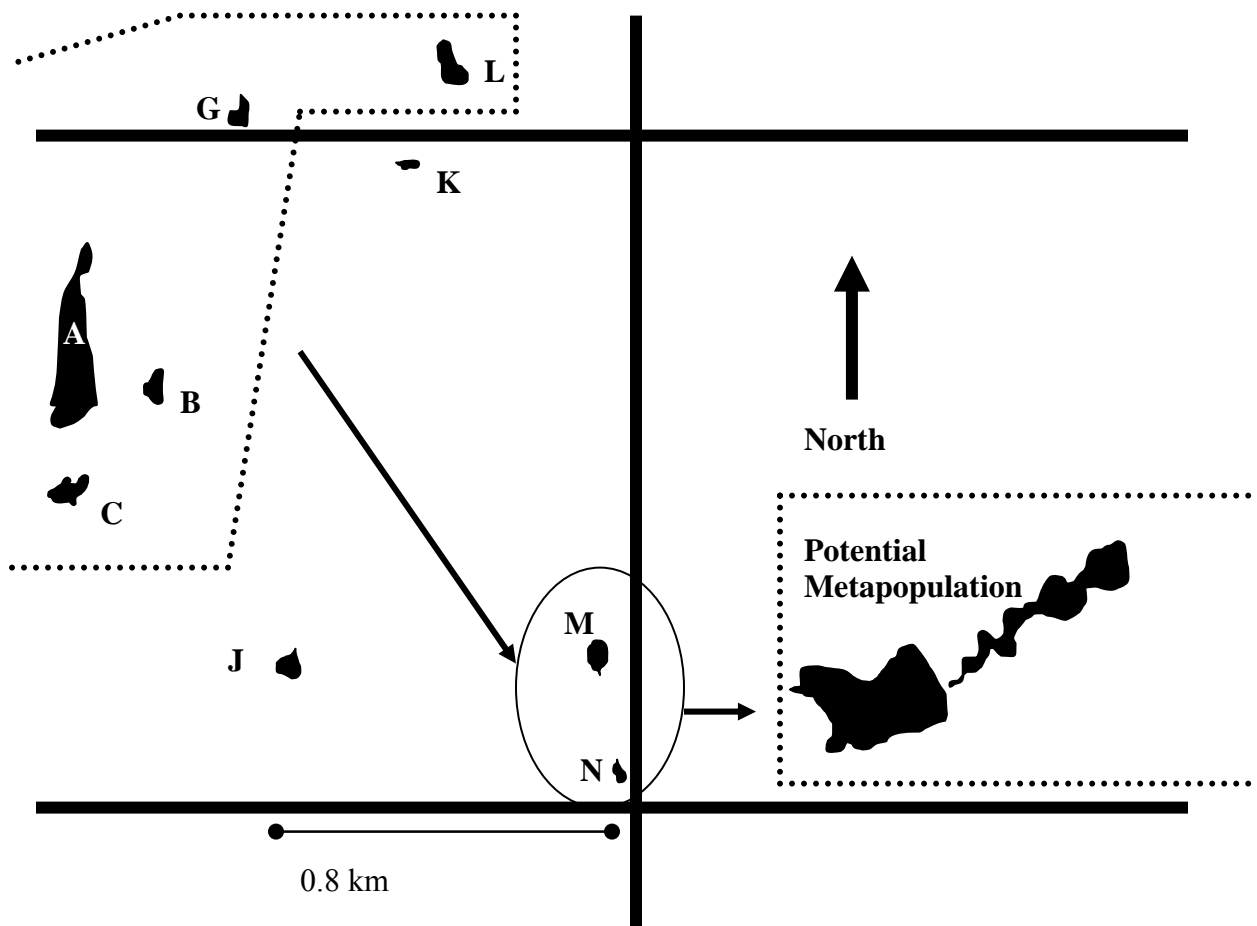


Figure 10. Eastern boundary of study site. Outside of the study site, approximately 3 km east of Pond A, is another large, permanent pond. Potentially, open populations M and N may be part of a neighboring metapopulation or used by migrants as corridors to connect the two metapopulations. Dotted lines denote hypothetical metapopulation boundaries.