Connectivity in an Agricultural Landscape as Reflected by Interpond Movements of a Freshwater Turtle

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Abstract: Connectivity is a measure of how landscape features facilitate movement and thus is an important factor in species persistence in a fragmented landscape. The scarcity of empirical studies that directly quantify species movement and determine subsequent effects on population density have, however, limited the utility of connectivity measures in conservation planning. We undertook a 4-year study to calculate connectivity based on observed movement rates and movement probabilities for five age-sex classes of painted turtles (Chrysemys picta) inhabiting a pond complex in an agricultural landscape in northern Virginia (U.S.A.). We determined which variables influenced connectivity and the relationship between connectivity and subpopulation density. Interpatch distance and quality of habitat patches influenced connectivity but characteristics of the intervening matrix did not. Adult female turtles were more influenced by the habitat quality of recipient ponds than other age-sex classes. The importance of connectivity on spatial population dynamics was most apparent during a drought. Population density and connectivity were low for one pond in a wet year but dramatically increased as other ponds dried. Connectivity is an important component of species persistence in a heterogeneous landscape and is strongly dependent on the movement behavior of the species. Connectivity may reflect active selection or avoidance of particular habitat patches. The influence of habitat quality on connectivity has often been ignored, but our findings highlight its importance. Conservation planners seeking to incorporate connectivity measures into reserve design should not ignore behavior in favor of purely structural estimates of connectivity.

Keywords: Chrysemys picta, habitat fragmentation, habitat quality, interpatch movement, multistate model, painted turtle

Conectividad en un Paisaje Agrícola Reflejada en Movimientos Entre Charcas de una Tortuga Dulceacuicola

Resumen: La conectividad es una medida de como el paisaje facilita el movimiento y por lo tanto es un factor importante en la persistencia de las especies en un paisaje fragmentado. Sin embargo, la escasez de estudios empíricos que cuantifiquen directamente el movimiento de especies y determinen los efectos subsecuentes sobre la densidad poblacional ha limitado la utilidad de las medidas de conectividad en la planificación de la conservación. Realizamos un estudio durante 4 años para calcular la conectividad basada en las tasas de movimiento observadas y las probabilidades de movimiento de cinco clases de sexo-edad de Chrysemys picta en un complejo de charcas en un paisaje agrícola en el norte de Virginia (E.U.A.). Determinamos las variables que influyeron en la conectividad así como la relación entre conectividad y la densidad subpoblacional. La distancia entre parches y la calidad del hábitat influyeron en la conectividad pero no las características de la matriz. Las tortugas hembras adultas fueron más influenciadas por la calidad del hábitat de las charcas recipientes que las otras clases de edad-sexo. La importancia de la conectividad en la dinámica poblacional

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espacial fue más aparente durante una sequía. La densidad poblacional y la conectividad fueron bajas en una charca en un año lluvioso pero incrementaron dramáticamente a medida que otras charcas se secaron. La conectividad es un componente importante de la persistencia de especies en un paisaje heterogéneo y depende estrechamente del movimiento de la especie. La conectividad puede reflejar selección activa o evasión de parches de hábitat particulares. La influencia de la calidad del hábitat sobre la conectividad a menudo ha sido ignorada, pero nuestros hallazgos resaltan su importancia. Los planificadores de conservación que buscan incorporar medidas de conectividad al diseño de reservas no deben ignorar el comportamiento a favor de estimaciones de conectividad puramente estructurales.

Palabras Clave: calidad de hábitat, Chrysemys picta, fragmentación de hábitat, modelo multiestado, movimiento entre parches

Introduction

Land conversion not only results in a decrease in the amount of original habitat but also alters the ability of an organism to move between remaining patches of natural habitat. This restriction of movement has potentially dire consequences for the persistence of species in fragmented habitats if movement rates are inadequate to prevent inbreeding, rescue declining populations, or recolonize vacant habitat (Fahrig & Merriam 1994; Calabrese & Fagan 2004). Therefore maintaining adequate movement rates is a central concern in conservation biology, as evidenced in the long interest in corridors (Rosenberg et al. 1997; Beier & Noss 1998; Haddad et al. 2003). For a corridor to be a successful conservation strategy, it must increase connectivity (the degree to which a landscape facilitates movement; Taylor et al. 1993).

The various methods with which to measure connectivity (reviewed in Calabrese & Fagan [2004]) differ primarily in whether connectivity is treated as a dependent or independent variable (Goodwin 2003) (i.e., whether connectivity is an attribute of the physical landscape or a measure of the functional response of individuals to the landscape template; Brooks 2003). Connectivity measures have been derived from characteristics of the landscape (e.g., interpatch distance; size, shape, and location of habitat patches; composition of matrix habitat), calculated by combining these physical features with limited data on movement ability of target species, or measured empirically by documenting movement between habitat patches. These approaches have been called structural, potential, and actual connectivity, respectively (Calabrese & Fagan 2004).

Determining actual connectivity is the most data-intensive approach and consequently is rarely performed (Goodwin 2003). A review of 106 empirical studies on spatially structured populations found that only 25 documented actual movement rates (Bowne & Bowers 2004). Movement rates are often explained as a function of the aforementioned landscape variables. Rarely has the quality of recipient habitat patches been factored into explanations of connectivity estimates. Movement among habitat patches beyond the home range is assumed to operate at too large a spatial scale for habitat selection to occur. But few empirically derived probabilities of interpatch movement have been calculated (but see Hestbesk et al. 1991; Spendelow et al. 1995; Hanski et al. 2000; Skvarla et al. 2004), so we know little about the factors influencing the destination of an emigrating individual. This deficiency is especially apparent in considering how movement behavior varies with ontogeny and sex (Johnson & Gaines 1990). Individuals may react differently to the same landscape based on costs and benefits specific to age and sex.

However it is measured, connectivity may be low in agricultural landscapes (Shepard & Swihart 1995; Gustafson & Gardner 1996), which often have numerous land-use types that constitute the matrix. This habitat diversity and the associated variety of habitat boundaries present a challenge to dispersing organisms. They are confronted not only with seasonally varying habitat qualities (i.e., the physical properties of a cultivated field vary dramatically from pre- to postharvesting), but also with strongly contrasting habitat edges, which may strongly influence individual behavior (Haddad 1999). Furthermore, farmers’ access to fields necessitates a strong network of roads, albeit ones with low traffic volume. Roads decrease connectivity directly through road-crossing mortality, but they also subtly influence behavioral changes (Forman et al. 2003).

Roads and other features of agricultural landscapes may strongly affect landscape connectivity for freshwater turtles. Vehicular collisions on roads are a source of great mortality in turtles, and that mortality may be biased toward adult females because of terrestrial nesting excursions (Marchand & Litvaitis 2004; Steen & Gibbs 2004; Aresco 2005; Gibbs & Steen 2005). Terrestrial activity is, however, not restricted to nesting by females. Numerous studies report terrestrial movement by freshwater turtles of both sexes (Cagle 1944; Sexton 1959; McAuliffe 1978; Morreale et al. 1984; Parker 1984; Gibbons et al. 1990). Differences in dispersal by males and females are still not completely understood. Males are hypothesized to perform long-range movements as a means to increase mating opportunities (Morreale et al. 1984; Gibbons et al. 1990). But Sexton (1959) reports that more adult females...
than males and more adults than juveniles travel between ponds.

We calculated actual connectivity over a 4-year period for painted turtles (*Chrysemys picta*) inhabiting ponds in an agricultural landscape in northern Virginia (U.S.A.). Because the risks and rewards of moving between habitat patches may vary by age and sex, we measured separate connectivity values for five age-sex classes. We sought to determine the degree of connectivity within a heavily managed landscape to elucidate which variables determine those levels of connectivity and investigate the relationship between connectivity and population density. We chose the painted turtle as a model organism because of its discrete habitat requirements, relative ease to mark, abundance, and long life. The painted turtle is also an important model species for the conservation of other freshwater turtles. Worldwide, roughly 45% of freshwater turtle taxa are listed as threatened in the 2000 IUCN Red List of Threatened Species (Turtle Conservation Fund 2002). By better understanding how a common freshwater turtle persists in a fragmented landscape, one can devise improved conservation strategies for the many imperiled freshwater turtle species.

**Methods**

**Study Species**

Adult painted turtles are size dimorphic: females are larger than males (mean ± SD carapace length in Virginia: 140 ± 12.9 mm vs. 120 ± 15.6 mm, respectively; Mitchell 1994). Age at maturity is variable, may be size dependent, and is found in Virginia to be 3–4 years for males (Mitchell 1985b) and 6 years for females (Mitchell 1985a). The painted turtle has been estimated to reach 40 years of age (Wilbur 1975).

Movement between ponds by the painted turtle is reported (Cagle 1944; Sexton 1959; McAuliffe 1978; Zweifel 1989). Seasonal movements have been observed for painted turtles in Michigan (Sexton 1959), Nebraska (McAuliffe 1978), and Illinois (Cagle 1944) and may have been prompted by the search for food resources. Empirical data that support or refute these claims, however, have not been collected. Several researchers found little evidence of interpond movement (Gibbons 1968; Bayless 1975; Mitchell 1988). This difference may be attributed to characteristics of the pond system studied. Movement did not occur in systems with isolated ponds but did occur when several ponds were in close proximity (~1000 m). Interpond movement is also more likely in drought conditions. Painted turtles typically leave a drying pond (Cagle 1944; Christiansen & Bickham 1989).

The spatial boundary of any population is difficult to delineate a priori (Camus & Lima 2002). For freshwater turtles the patchy nature of pond habitats superficially suggests a metapopulation (Levins 1970), with each pond housing a demographically independent subpopulation. A single habitat patch (i.e., a pond) may or may not house a subpopulation (Pannell & Obbatt 2003). At sufficiently large spatial scales a population can be considered closed but spatially patchy, with movement occurring between habitat patches within a single “patchy population” (Harrison 1991; Hixon et al. 2002). Burke et al. (1995) claim that a metapopulation of slider turtles encompassed habitats 3.5 km from a central wetland, but it is unclear whether this was an example of a classic metapopulation (Levins 1970) or a spatially disjunct patchy population (Harrison 1991). The results of our study will help guide the delineation of the population in this landscape.

**Study Site**

We conducted a mark-recapture study from 1998 to 2001 in and around Blandy Experimental Farm (BEF) in northern Virginia (78°3’40”W, 39°5’40”N). Our focal study area consisted of nine ponds (Fig. 1) that have existed since at least 1937. The ponds, separated by distances ranging from 110 to 2300 m, were within a single, easterly flowing drainage in an agricultural landscape (Fig. 1; see Bowne [2002] for complete site description). Four

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**Figure 1.** Landscape characteristics of the painted turtle study site. Numbers are the ponds studied (1, Jones Pond; 2, Callahan Pond; 3, Lake Georgette; 4, Rattlesnake Spring; 5, Lake Arnold; 6, Drainage Pond; 7, Border Pond; 8, Center Pond; 9, East Pond). Only Jones Pond, Rattlesnake Spring, and Center Pond retained water after 1998.
ponds (Jones, Border, Center, and East) were on active cattle farms beyond the borders of BEF. In the autumn of 1998, a drought dried all but three ponds (Jones, Center, Rattlesnake). Low rainfall persisted throughout the remainder of the study. Rattlesnake Spring held water for most of the trapping seasons but dried in mid- to late August of 1999, 2000, and 2001. We occasionally sampled more distant ponds (n = 12) to check for emigrants from the focal area and mark potential immigrants.

Study Design

We captured turtles with hoop traps (Nylon Net Company, Memphis, Tennessee) baited with sardines from mid-April to mid-September of each year. In 1998 traps were set every week for 2 consecutive days in nine ponds. In 1999–2001, traps were set every 2 weeks for 3 consecutive days in the three ponds (Jones, Center, Rattlesnake) that retained or regained water (Fig. 1).

At each capture we measured the length of plastron, right third foreclaw, and precloacal tail with dial calipers and weighed the individual with a Pesola hanging scale (Baar, Switzerland). Sex and number of annuli were also recorded. We classified each turtle into one of five age-sex classes (adult male, adult female, subadult male, subadult female, and juvenile) and gave each individual a unique identification code by filing marginal scutes. A turtle could only be in one age-sex class per year but could change classes between years. Individuals with the length of the third right foreclaw of ≥10 mm were considered adult males (Frazer et al. 1993). Adult females were those whose plastron length exceeded 106 mm (Mitchell 1985a). Subadults of both sexes possessed at least three annuli and males were differentiated from females by their longer precloacal tail, longer foreclaws, and less domed carapace. Juveniles were any turtle with two or fewer annuli.

We calculated individual growth rates of immature turtles by pond (Rattlesnake, Jones, and Center) to estimate relative habitat quality. Growth rates of individuals vary between habitats of different productivities (Sexton 1959; Gibbons et al. 1978, 1981; McAuliffe 1978; Brown et al. 1994). By increasing growth rate, juveniles can more quickly escape size-dependent mortality and may obtain sexual maturity faster (Ernst 1971; Congdon et al. 1992; Frazer et al. 1993). By definition, higher-quality ponds yielded faster growth rates. Painted turtles grow only when water temperature is consistently above 15°C (Sexton 1965), a requirement reached between 31 May and 31 August in our study system (Bowen 2002). Therefore, only successive captures within a single pond over this 3-month period were used in calculating growth rates. Individual relative growth rates were calculated according to Andrews (1982):

\[ K = (\ln S_2 - \ln S_1)/(t_2 - t_1) \]

where \( S_1 \) and \( t_1 \) are the turtle size and time at the first measurement and \( S_2 \) and \( t_2 \) are the size at and time of next measurement, respectively.

We estimated relative habitat quality for adult females by comparing clutch attributes among ponds. Reproductive output of turtles is linked to habitat productivity (Brown et al. 1994; Kennett 1999). Larger clutches or a greater proportion of gravid individuals indicate better habitat. Because painted turtles acquire the resources for reproduction in the summer prior to egg laying (Congdon & Tinkle 1982), we assessed habitat quality for the pond in which the turtle was located in the previous year. During the nesting season (late May to early July), mature females were x-rayed to determine clutch size (Gibbons & Greene 1979). This technique appears to be safe for developing turtle embryos (Hinton et al. 1997).

We also used radiotelemetry to track the movement of individual turtles. Radiotelemetry is an effective complement to mark-recapture studies in that more detailed information can be obtained. It is limited, however, in sample number and size of individuals to be tracked. We attached radiotransmitters (Advanced Telemetry Systems, model 7PN, Isanti, Minnesota) to 60 adult turtles (n = 25 in 1999, all females; n = 14 in 2000, 9 males, 5 females; n = 21 in 2001, 10 males, 11 females) distributed evenly over the three focal ponds (Jones, Rattlesnake, Center). From mid-June to the end of August, we obtained a daily location for each turtle by homing to its exact position. We then recorded each location on an aerial photograph and later digitized it into a geographic information system (GIS) with ArcView (ESRI, Redlands, California).

Statistical Analysis

We analyzed actual connectivity values in three forms, two of which (movement rate and movement probability) were concerned with age- and sex-specific movement between pairs of pond, and the third (pond specific connectivity) with a specific pond. At the pond level, connectivity for pond j in each time period was determined by dividing the total number of immigrants into j by the total immigrant pool (excluding emmigrants from j). Data were summed across age-sex classes.

Within a given year, we used a multistate model with Pollock’s robust design model (MSSRVD) to calculate biweekly movement probabilities and survival estimates for each age-sex class (Hines 2001; Skvarla et al. 2004). A multistate model estimates transition probabilities between different locations (Nichols & Kendall 1995). Pollock’s robust design allows for improved estimates of capture probability and survival (Pollock & Otto 1983). It consists of two capture periods, differentiated by time elapsed between trapping efforts. The primary periods are trapping efforts separated by sufficiently long time intervals (12 days in this study) in which birth, migration, or mortality can occur. Trapping within the secondary period is conducted...
over a sufficiently short timeframe (3 days in this study) such that the system is considered closed to birth, migration, or mortality. An interpond movement is the unit of observation in this analysis and not the individual. Fortunately, only six turtles made more than one interpond movement within a year. The MSSRVRD was modified to incorporate differences among groups.

Known histories of turtles with radiotransmitters were incorporated into estimates of capture and movement probabilities. Because status (alive or dead) and location are known at each trapping occurrence for radio-marked turtles, movement rates are known for these animals. This increases the sample size going into the estimates of movement rates without adding estimation error, yielding more precise movement-rate estimates.

The adequacy of each model to describe the data was tested with a goodness-of-fit test. Model selection was based on Aikake information criteria (AIC), with the better model having the lowest value. Although not a statistical test, we considered AIC values differing by 2 to be significantly different (Spendelow et al. 1995).

We categorized data on movement behavior across years by the last known location at time \( t \) to first known location at time \( t \). We calculated a connectivity value of movement rate for \( ij \) pairs of ponds by dividing the total number of observed immigration events into pond \( j \) by the total number of recaptured individuals of each age-sex class from the origin pond \( i \). Because this approach requires the lumping of trapping records from many different trapping occasions into only two time periods (\( t, t - 1 \)), we decided against formally calculating movement probabilities. This method underestimates movement because it does not consider those individuals that moved but were not caught. If capture probabilities are equal among ponds and sexes, however, the results will not be biased. This assumption is realistic because trapping was performed over a long period and an individual need only be recaptured once. We tested the null hypothesis that movement did not differ among time periods with a \( 2 \times 7 \) chi-square contingency table (2 behavioral states, 7 time periods).

In estimating habitat quality, we pooled data on growth rates across years (1999, 2000, 2001) to increase sample size. Too few immature turtles were recaptured within individual ponds in 1998 to be included in the analysis. Growth rates were analyzed separately for juveniles, subadult males, and subadult females with a one-way analysis of variance (ANOVA) with pond as the independent variable. We performed post hoc multiple comparisons with Scheffe’s test. Data were square-root transformed.

We also pooled clutch data across years. For females measured in multiple years, data for a random single year were selected to ensure independence of observations. We excluded turtles that were caught in more than one pond. Clutch sizes were square-root transformed and analyzed with a one-way analysis of covariance (ANCOVA), with prior-year pond as the independent variable and plastron length as a covariate. Comparisons of the proportion of gravid individuals in each of the three ponds were tested with a \( 2 \times 3 \) chi-square contingency table (2 gravid states, 3 ponds).

We estimated population size in each pond at each trapping period with Pollock’s robust design (Pollock & Otto 1983) and Huggins’ estimator in the program MARK (White & Burnham 1999). Population size was divided by pond surface area to obtain a density estimate. Surface areas of ponds were calculated from digital orthophotos with a geographic information system (ArcInfo, ESRI, Redlands, California).

**Results**

We made a total of 4490 captures of 725 turtles within the study area from 1998 to 2001. Of the 527 recaptured turtles, 245 (46%) moved among ponds. The proportion of individuals that moved within each time period was significantly different among time periods (\( \chi^2_{20} = 439.26, \ p < 0.05 \)). Movement rates were highest in 1998 (29%) and between 1998 and 1999 (61%).

Pond-specific connectivity values for the three ponds that retained water (Jones, Rattlesnake Spring, and Center) varied considerably over the course of the study (Fig. 2). Straight-line distances traversed to the permanent ponds ranged from 230 to 1220 m. A significant difference in number of immigrants to each of the permanent ponds was detected (\( \chi^2_{14.3} = 117.2, \ p < 0.01 \)). Rattlesnake Spring had no actual connectivity in the wet year of 1998. Its pond connectivity value increased dramatically when it was only one of three ponds remaining (Fig. 2). In the 1998–1999 interval, the connectivity of Rattlesnake Spring was significantly higher than the other two permanent ponds (\( \chi^2_{14.3} = 14.3, \ p < 0.01 \)). Jones and Center ponds had fairly consistent connectivity values over the course of the study, with means (±SD) of 0.30 ± 0.06 and 0.56 ± 0.15, respectively (Fig. 2).

![Figure 2. Pond-specific measures of landscape connectivity for painted turtles among the three ponds that existed for the duration of the study.](image-url)
The best-fit model for each age-sex class was when survival, closed-model capture probabilities, and transition probabilities were held constant over time and strata (Table 1). During the 1998 field season, adult turtles had the most diverse movement probabilities (Table 2). Jones and Center ponds received the bulk of immigrants (Table 2). Again, no turtles moved to Rattlesnake Spring. Movement to the nonpermanent ponds was possible only in 1998 and occurred in low numbers from Center to East (230 m), Arnold to Georgette (587 m), and Drainage to Arnold (446 m) (Table 2). Movement probabilities were low (0.00 in most cases) in 1999, 2000, and 2001 for turtles emigrating from Jones and Center ponds (Table 3). Movement probabilities were higher for turtles emigrating from Rattlesnake Spring and were usually equal toward Jones and Center ponds (Table 3).

High movement rates occurred between 1998 and 1999 as turtles departed from drying ponds (Fig. 3). Movement rates for each age-sex class, except adult females, were highest toward the closest permanent pond. Adult females continued to avoid Rattlesnake Spring (Fig. 3c). Movement rates to Rattlesnake Spring continued to be low in later time periods (Fig. 4).

During the 3 years of radiotelemetry work, 14 turtles dispersed up to 3300 m; 12 of them successfully found aquatic habitat. Cars killed the remaining 2 turtles. Two of

Table 2. Transition matrix of movement probabilities (±SE) of painted turtles among ponds in 1998 for each age-sex class.*

<table>
<thead>
<tr>
<th>Class</th>
<th>Origin pond</th>
<th>Jones</th>
<th>Georgette</th>
<th>Arnold</th>
<th>Center</th>
<th>East</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adult female</td>
<td>Callahan</td>
<td>0.04 ± 0.05</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>Georgette</td>
<td>0.03 ± 0.02</td>
<td>0.97 ± 0.02</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>Arnold</td>
<td>0.00</td>
<td>0.04 ± 0.02</td>
<td>0.92 ± 0.02</td>
<td>0.04 ± 0.02</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>Center</td>
<td>0.00</td>
<td>0.00</td>
<td>0.96 ± 0.03</td>
<td>0.04 ± 0.03</td>
<td>0.04 ± 0.03</td>
</tr>
<tr>
<td></td>
<td>East</td>
<td>0.00</td>
<td>0.00</td>
<td>0.31 ± 0.13</td>
<td>0.69 ± 0.13</td>
<td>0.69 ± 0.13</td>
</tr>
<tr>
<td>Adult male</td>
<td>Callahan</td>
<td>0.14 ± 0.08</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>Georgette</td>
<td>0.03 ± 0.01</td>
<td>0.00</td>
<td>0.03 ± 0.01</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>Arnold</td>
<td>0.03 ± 0.01</td>
<td>0.00</td>
<td>0.94 ± 0.01</td>
<td>0.03 ± 0.01</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>Drainage</td>
<td>0.00</td>
<td>0.00</td>
<td>0.16 ± 0.06</td>
<td>0.16 ± 0.06</td>
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<tr>
<td></td>
<td>East</td>
<td>0.00</td>
<td>0.00</td>
<td>0.16 ± 0.06</td>
<td>0.84 ± 0.06</td>
<td>0.84 ± 0.06</td>
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<tr>
<td>Subadult male</td>
<td>Center</td>
<td>0.00</td>
<td>0.00</td>
<td>0.96 ± 0.03</td>
<td>0.04 ± 0.03</td>
<td>0.04 ± 0.03</td>
</tr>
<tr>
<td>Juvenile</td>
<td>East</td>
<td>0.00</td>
<td>0.00</td>
<td>0.36 ± 0.29</td>
<td>0.64 ± 0.29</td>
<td>0.64 ± 0.29</td>
</tr>
</tbody>
</table>

*Results are based on the recaptures of 44 adult females, 49 adult males, 14 subadult females, 28 subadult males, and 20 juveniles.
21 (9.5%) turtles emigrated 1700 m from Jones Pond to a pond outside the focal area, and 1 of these subsequently returned to Jones Pond. Ten of 18 (55.0%) turtles left Rattlesnake Spring. Four of these moved to Center Pond (1000 m), and the remaining 6 moved to one of three more distant ponds (range: 2500–3300 m). These turtles remained in the pond to which they immigrated. Of the 21 turtles equipped with a radiotransmitter in Center Pond, all remained in that pond.

Pond quality, based on growth rates, significantly differed for juveniles ($F_{2,77} = 3.33, p = 0.04$; Jones, $n = 44$; Rattlesnake, $n = 13$; Center, $n = 23$) and subadult females ($F_{2,102} = 12.2, p < 0.01$; Jones, $n = 43$; Rattlesnake, $n = 11$; Center, $n = 51$) but not for subadult males ($F_{2,56} = 1.64, p = 0.20$; Jones, $n = 30$; Rattlesnake, $n = 9$; Center, $n = 20$). The slowest growth rate for juveniles was in Rattlesnake Spring but was significantly different only from Jones Pond ($p = 0.04$). For subadult females, Rattlesnake Spring produced significantly lower growth rates than both Jones ($p < 0.01$) and Center ponds ($p < 0.01$). Subadult males also had the lowest growth rates in Rattlesnake Spring, but these rates were not statistically different from the other two ponds.

A total of 111 C. picta were x-rayed, but the prior-year location was known for only 79 turtles (Jones, $n = 17$; Rattlesnake, $n = 8$; Center, $n = 54$). Of these, 29 turtles were gravid (Jones, $n = 7$; Rattlesnake, $n = 2$; Center, $n = 20$). Significant differences among ponds were detected for proportion of gravid individuals ($\chi^2_{0.05,2} = 6.16, p < 0.05$; Jones = 0.41, Rattlesnake = 0.25, and Center = 0.37) but not for clutch size ($F_{2,25} = 0.87, p = 0.43$). Length of plastron was also not significantly related to clutch size ($F_{1,25} = 0.42, p = 0.52$).

Mean (±SD) population densities (turtles/ha) in 1998 were highest in the permanent ponds, except Rattlesnake Spring (Jones: 129 ± 79; Center: 294 ± 93; Rattlesnake: 0). The drying of the ephemeral ponds in autumn of 1998 caused a subsequent rise in mean population densities in the remaining three ponds in 1999 (Jones: 497 ± 183; Center: 911 ± 350; Rattlesnake: 2648 ± 1318). Few individuals, however, left either Jones or Center ponds (Tables 2 & 3, Figs. 3 & 4). After the initial impact of the mass drying of ponds, the effects of movements became less apparent on the population density in Center and Jones ponds. In contrast, Rattlesnake Spring exported more individuals than it gained; consequently, population density declined each year.

A total of 394 turtles were captured in the 12 ponds surrounding the focal study area. Twenty-six of these turtles were emigrants from the focal study area. Additionally, two marked turtles immigrated to the focal study area. The numbers of emigrants varied by age and sex but the distances moved were fairly similar (mean ± SD: 2447 ± 303 m).

Table 3. Transition matrix of movement probabilities (±SE) of painted turtles among existing ponds in 1999, 2000, and 2001 for each age-sex class.*

<table>
<thead>
<tr>
<th>Class</th>
<th>Year</th>
<th>Origin pond</th>
<th>Destination pond</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Jones</td>
</tr>
<tr>
<td>Adult female</td>
<td>1999</td>
<td>Rattlesnake</td>
<td>0.02 ± 0.02</td>
</tr>
<tr>
<td></td>
<td>2000</td>
<td>Rattlesnake</td>
<td>0.04 ± 0.02</td>
</tr>
<tr>
<td></td>
<td>2001</td>
<td>Jones</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Rattlesnake</td>
<td>0.98 ± 0.02</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Center</td>
<td>0.05 ± 0.03</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Rattlesnake</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Center</td>
<td>0.00</td>
</tr>
<tr>
<td>Subadult female</td>
<td>1999</td>
<td>Jones</td>
<td>2:3</td>
</tr>
<tr>
<td></td>
<td>2000</td>
<td>Rattlesnake</td>
<td>4:18</td>
</tr>
<tr>
<td></td>
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<td>0.00</td>
</tr>
<tr>
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<td>0.00</td>
</tr>
<tr>
<td></td>
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<td>0.01 ± 0.01</td>
</tr>
<tr>
<td></td>
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</tr>
<tr>
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<tr>
<td></td>
<td>2001</td>
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</tr>
<tr>
<td></td>
<td></td>
<td>Center</td>
<td>0.04 ± 0.03</td>
</tr>
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</table>

*A ratio of the number of individuals behaving in a certain manner (remaining in pond or moving between a pair of ponds) to the total number of individuals recaptured within the pond of origin is given when a movement probability could not be calculated because of poor model fit. Sample sizes (in 1999, 2000, 2001, respectively) are adult females, 79, 80, 93; adult males, 56, 70, 77; subadult females, 11, 54, 62; subadult males, 20, 39, 37; and juveniles, 42, 44, 41.
Discussion

Connectivity is typically treated as a property of the landscape, with interpatch distance often modeled as the major determinant of connectivity (Goodwin & Fahrig 2002). Our measures of actual connectivity indicated that interpatch distance was important, but, for certain age-sex classes, not as important as habitat quality. For example, movement to the most centrally located pond, Rattlesnake Spring, was not detected when other ponds were available. Its habitat quality was lower than that of other permanent ponds. Only after a drought caused the drying of most ponds did Rattlesnake Spring achieve a high degree of connectivity. This finding emphasizes the importance of placing actual connectivity values in context of when and for whom they were measured. This high level of connectivity did not hold for all age-sex classes. From 1998 to 1999, adult female painted turtles continued to avoid Rattlesnake Spring and moved to ponds at least 7.5 times more distant. This suggests that habitat selection occurred and that habitat quality needs to be factored into estimates of connectivity.

Rarely has habitat quality been factored into structural estimates of connectivity. This is partly because habitat quality is difficult to assess without detailed, empirical information but also because the scale at which connectivity is measured is assumed to be too great for habitat selection to occur. Most connectivity studies implicitly assume that interpopulation movement is occurring. It follows then that individuals will not have prior knowledge of habitat patch quality and will be more influenced by variables such as interpatch distance, habitat patch size and shape, and matrix composition. This assumption is difficult to test, especially for long-lived organisms, because of the large amount of data required. But ignoring patch quality may prevent an accurate interpretation of factors influencing connectivity. Haynes and Cronin (2004) report that matrix composition and patch quality often covary, making it difficult to separate the effects of the matrix from that of patch quality. Still, several researchers report effects of habitat quality on movement rates (Smith & Peacock 1990; Verboom et al. 1991; Spendelow et al. 1995; Muller et al. 1997; Verhulst et al. 1997).

The rate of movement between ponds in our study suggests that each pond does not contain a demographically independent population, but neither is movement so frequent as to make interactions between all individuals equally likely (e.g., few individuals moved between...
Jones and Center ponds). Painted turtles moved freely between ponds but did so on the order of once per year, as evidenced by both recapture and telemetry data. The spatial scale of our study system is intermediate between that of a home range and that of long-distance dispersal; it most closely resembles the “patchy population” designation (Harrison 1991). Consequently the relative degree of knowledge that an individual possesses on habitat quality is intermediate between omniscience of local sites and complete ignorance of the landscape. This informational content helps explain the relative roles of habitat quality and distance on influencing the destinations of immature and mature turtles.

Mature turtles are likely to possess greater knowledge of the location and relative quality of ponds within the immediate landscape (Zweifel 1989) and may satisfy the omniscient assumption of most habitat-selection models (Oksanen et al. 1995). They more effectively chose higher quality habitat over greater distances. Furthermore, the physiological costs and predation risks of terrestrial exposure for mature painted turtles, especially for the larger adult females, are lower than those for the smaller, immature turtles (Lefevre & Brooks 1995; Finkler 2001). The observed movement patterns of juveniles could be a result of increased cost of traveling to distant ponds (Pyke et al. 1977) or of simply not knowing that more distant ponds exist. Consequently, immature turtles are severely limited in their ability to select the best habitat and are less able to respond to unfavorable environmental conditions. So in designing a refuge system or devising a management plan, one needs to pay attention to how connectivity differs by age and sex. Adult female painted turtles were evidently more willing to move greater distances, and this behavior placed them at greater risk of vehicular collisions.

Roads were the only feature of the landscape matrix that measurably affected connectivity for the painted turtle because painted turtles maintain nearly straight movement paths regardless of habitat type or edge (Bowne & White 2004). A four-lane highway that marked the north edge of the study system appears to be a complete barrier to movement (Bowne & White 2004), as evidenced by the tracked turtle that was killed by a car. Turtle mortality on roads poses a major threat to the persistence of turtle populations (Gibbs & Shriver 2002; Steen & Gibbs 2004; Aresco 2005).

Our finding that turtles move fairly often and relatively great distances suggests that painted turtles may be at a greater risk of traffic mortality than believed. Gibbs and Shriver (2002) use average distances moved for nesting (100 m) to model mortality risk for painted turtles and found little risk at the modeled road density. But our data indicate that painted turtles move much greater distances and would be at greater risk than that supposed only by nesting distances. This is especially true during times of drought. Our results were affected strongly by a drought that prompted a great number of movements of 1450 m. Mass emigration of freshwater turtles induced by pond drying is reported in several studies (Gibbons et al. 1983; Buhlmann 1995; Morales-Verdeja & Vogt 1997). But turtles may emigrate even when habitat is not actively degrading, as evidenced by movement from the permanent ponds.

Movement between ponds is of vital importance for the persistence of this patchy population (Harrison 1991). The spatially patchy nature of a population may not appear important if one aggregates data across habitats to examine overall population dynamics. Treating the total population as an aggregate of subpopulations, however, ignores potentially important patch-level processes (i.e., source-sink dynamics, Pulliam 1988). Distinguishing source and sink habitats is especially important in conservation. Conservationists and natural resource managers need to know which habitats are high-priority areas in terms of contribution to regional population dynamics (Pulliam 1996; Fauth 2001; Murphy 2001). This line of inquiry places the importance on the patchy nature of the population. In our study not all the ponds were of equal importance. The drought highlighted the need to ensure
protection of those habitats that are refugia in time of environmental stress. The two most important ponds (Jones and Center) for the turtle population existed on private land. We agree with Joyal et al. (2001) that a pond complex, not an individual pond, should be the habitat unit of conservation.

We argue that connectivity is a function of the behavior of individuals in relation to landscape features and habitat quality. It is a dependent variable. Conservation planning that incorporates connectivity should be based at least partially on known behavior of the target species. Purely structural connectivity values (Calabrase & Fagan 2004) have little value if they are calculated without regard to the ecology of the organism. Formulations of connectivity should include those elements that constitute the quality of habitat.

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