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Genetic Diversity of the Brownsville Common Yellowthroat (*Geothlypis trichas insperata*)

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Genetic Diversity of the Brownsville Common Yellowthroat (*Geothlypis trichas insperata*)

A THESIS

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ABSTRACT OF THESIS

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ABSTRACT:

Habitat fragmentation is particularly severe in the Lower Rio Grande Valley (LRGV) of south Texas, where an estimated 95% of the native brushland has been eliminated by agriculture and urban development. This fragmentation effectively divides bird populations into smaller "subpopulations within a population," or a metapopulation. Fragmentation has divided wetland habitat where wetlands are more dense close to the Rio Grande River and becomes more scattered north of the River. Therefore, bird species who utilize the wetlands close to the River should be denser and more closely related, genetically, than individuals farther north. A good model for studying the effects of fragmentation in the LRGV is the "Brownsville" Common Yellowthroat

(*Geothlypis trichas insperata*), a subspecies of the Common Yellowthroat. Klicka (1994) studied the Brownsville Common Yellowthroat and concluded that they were restricted to the southern third of Cameron County and they were most common along the Rio Grande River. Several predictions were tested. (1) Apparent survivorship of Brownsville Yellowthroats in the LRGV has not changed since the 1988-1989 study conducted by Klicka (1994). (2) Linear density of Brownsville Yellowthroats is greatest nearer to the River. (3) I expect individuals on or near the Rio Grande River to be more closely related than northern individuals. (4) The source-sink metapopulation model should be the model best fit to describe this subspecies. Blood samples were collected from captured individuals (n = 128) for microsatellite testing. Samples were examined with a genetic analyzer and subjected to tests using programs STRUCTURE, CERVUS, GENEPOP, and RELATEDNESS. Apparent survivorship for this study (34%) was lower than that reported by Klicka (55%; 1994). The linear densities of sites near the Rio Grande River and far from the River were not significantly different. Analysis of genetic relatedness indicates that individuals are as related to each other as would be expected in distant relatives. Therefore, these data indicate that a single, admixed population is present in the LRGV which most closely resembles an open population model.

I. INTRODUCTION

Population Dynamics

The dynamics of animal populations can be studied using three basic models (closed, open, and metapopulation). The closed population models assume that no individuals enter or leave the population (Kendall 1999). In a closed population, some barrier (e.g. spatial, behavioral, or temporal) restricts gene flow from occurring (Allaby 2003). The population remains consistent for the duration of the study without any known changes from the initial population such as births or immigrants and death or emigrants (White et al. 1982). An open population model, on the other hand, tolerates permanent additions to (e.g. immigration) and deletions from (e.g. emigrations) the populations under study, as boundaries are more permeable than those seen in a closed model (Jolly 1965; Seber 1965). In an open population, there is no barrier to gene flow (Allaby 2003).

The metapopulation model is used for any spatially-structured population. Metapopulation theory generally describes groups of the same species who are spatially separated into local populations, islands, or subpopulations (Hanski 1998). Although derived from the theory of island biogeography, which pertains to sets of species (MacArthur and Wilson 1967), metapopulation theory applies to populations of the same species. Levins (1969) describes a metapopulation as a “population of populations” and coined the term “metapopulation”. These subpopulations can survive relatively independent of one another but still interact

to some degree (Barton and Whitlack 1997). Thus, the metapopulation could be loosely considered an aggregation of interconnected open subpopulations. The classical metapopulation structure of Levins (1969) describes subpopulations that are in a balanced state of extinction and recolonization that is driven by dispersal of individuals or species and gene flow between subpopulations. The subpopulations have continual fluctuations in size, such as increases due to immigration and births as well as decreases caused by deaths and emigration (Pulliam 1988). New immigrants to an area may increase the size of the current subpopulation or repopulate an extinct subpopulation that previously was inhabitated (Gurevitch et al. 2006). So, despite fluctuations at the subpopulation level, the metapopulation remains relatively stable (Hanski and Simberloff 1997; Gurevitch et al. 2006). Therefore, it can be inferred that a subpopulation is at higher risk of extinction when the number of individuals within the subpopulation is reduced. Because there are interactions among subpopulations, constant losses of subpopulations will likely result in the elimination of the entire metapopulation (Nee and May 1992).

Metapopulation theory can be a useful tool when examining population dynamics, population ecology, conservation, genetics, evolution, and population interactions (Hanski 1994, 1999; Esler 2000; Hanski and Ovaskainen 2003). Metapopulation models work well when subpopulations are spatially separated on a small scale (Gurevitch et al. 2006). The degree of isolation between populations of the same species, genetic distinctiveness, risk of extinction, and contribution to the subsistence of the species are some of the many aspects that

should be accounted for in conservation efforts (Bouzat et al. 2009). Changes in the population size of a species can be estimated from models developed from the metapopulation theory (Gurevitch et al. 2006). Some systems in which metapopulation models have worked include: plant communities in serpentine soils (Kruckeberg 1954; Whittaker 1954), tallgrass prairie communities (Gotelli and Simberloff 1987; Collins and Glenn 1990, 1991), amphibians like the Red-spotted Newt *(Notophthalmus viridescens*) occurring in mountain ponds of Virginia (Gill 1978a, 1978b) and the Pool Frog (*Pelophylax lessonae*) in Sweden (Sjogren-Gulve 1994), Glanville Fritillary (*Melitaea cinxia*) on the Aland Islands of Finland (Hanski et al. 1994, 1995), parasites/host-pathogen and bacteria (Thrall and Antonovics 1995; Ebert et al. 2001; Lopez et al. 2005; Ganz and Washburn 2006; Keymer et al. 2006), organisms associated with archipelago systems (MacArthur and Wilson 1967), as well as numerous bird species (Buckley and Downer 1992; Wooton and Bell 1992; Opdam et al. 1994; Gutierrez and Harrison 1996; Smith et al. 1996; Stith et al. 1996)

However, there are cases where a metapopulation model is not the most appropriate model to use. For example, metapopulation processes do not appear to be useful when studying plant communities at large scales (Scheiner and Rey-Benayas 1994). Additionally, it can be difficult to differentiate local populations in a marine environment and define their spatial scales (Grimm et al. 2003). The metapopulation concept is not applicable if either of two circumstances is present in the population. First, dispersal rates are high enough that subpopulations never experience extinctions, resulting in a large continuous

population rather than smaller discrete subpopulations. Second, in determining population size and distribution, migration and extinction rates are too low and do not influence the dynamics of the population (Gurevitch et al. 2006). To sum up, directional dispersal must be present to a measurable extent in the metapopulation, but individuals cannot move so freely that subpopulations meld into a completely panmictic population. Most populations have barriers to dispersal and develop subpopulations with varying levels of gene flow and isolation. Therefore, a metapopulation model is (usually) an adequate method to describe the interaction between the individuals within the population.

There are two model variations, source-sink and patchy (Harrison 1991), derived from the classical metapopulation model. The source-sink model (Figure 1) applies to metapopulations where discrete subpopulations experience directional movement of individuals from a source to sinks (Keitt et al. 1995). A "source" is an area where additions (births) outweigh the removal (mortality and emigration) of individuals (Pulliam 1988). As a result, the population increases. A "sink" describes an area that does not have the reproductive surpluses to offset loss of individuals due to mortality and emigration (Pulliam 1988). Therefore, to persist, sink populations rely heavily on the addition of new individuals, specifically, the constant immigration of recruits from a source area (Gurevitch et al. 2006). If the source generates excess individuals that regularly move to sinks, the sinks can theoretically persist perpetually (Keitt et al. 1995). Emigrants can move from source to sinks and rescue local sink populations from extinction, a phenomenon known as "rescue effect" (Brown and Kodric-Brown 1977;

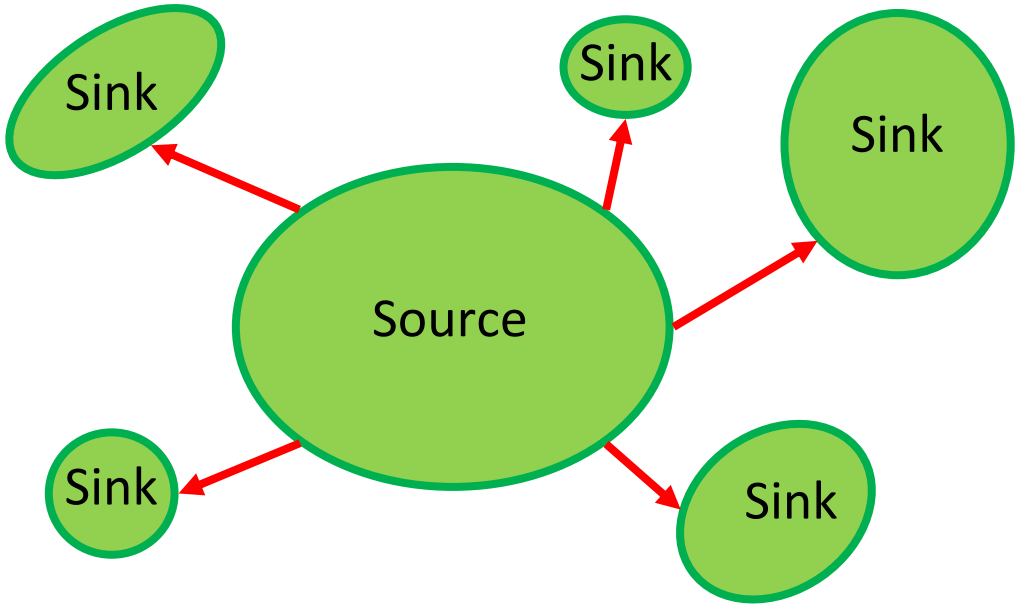

FIGURE 1. Source-sink metapopulation model where individuals move from an area in which additions outweigh deletions (source) to areas that do not have surplus individuals (sink) to counter the high rate of deaths or immigration.

Coulton and Clark 2008). However, if a source is eliminated with no local population to take its place, the satellite sink populations are at risk of going extinct as well. It also is plausible that source populations rotate over time where a sink becomes a source and a source is reduced to a sink. This idea is suggested in a study estimating migration rates, population size, demographics, and dynamics in a metapopulation of Northern Goshawks (*Accipiter gentilis*) in southeastern coastal Alaska (Sonsthagen et al. unpublished). If a source area becomes unsuitable and the number of available recruits diminishes, a previously unstable sink population may improve and have the capacity to provide recruits

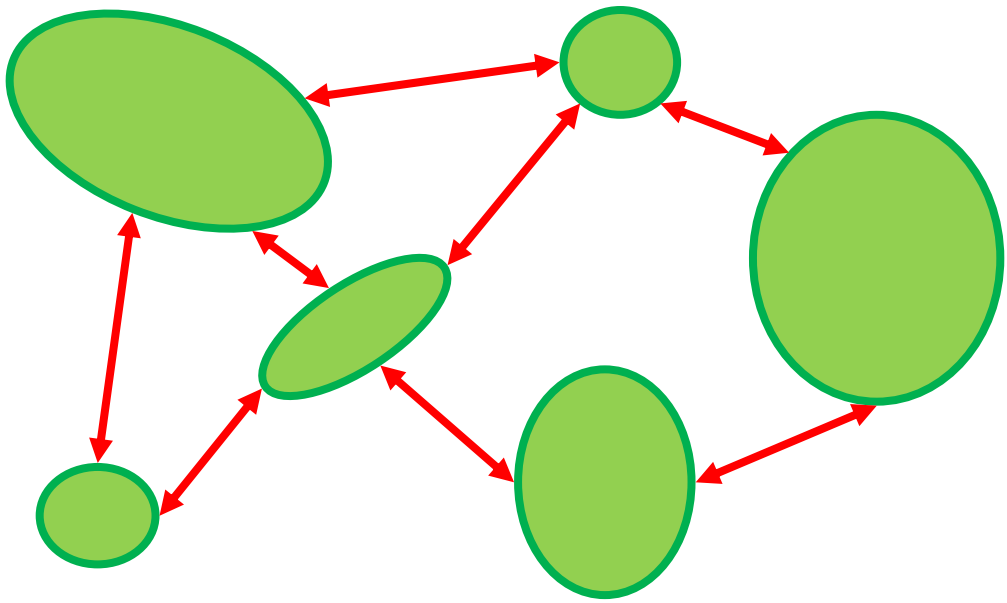

FIGURE 2. Patchy metapopulation model where individuals move freely among local populations. Even though subpopulations exist, individuals are highly mobile, making this assemblage appear to be a large, single population.

to neighboring populations, resulting in rotating source populations (Coulton and Clark 2008).

Subpopulations with high dispersal potential and migrants that move evenly between patches characterize a patchy metapopulation model (Figure 2; Harrison 1991). In this model, subpopulations function as a well-mixed, single, large population where individuals “belong” to more than one subpopulation (Keitt et al. 1995; Bowne and Bowers 2004). Unlike the source-sink model, the patchy model does not take local population extinction into consideration (Harrison 1991). The entire population survives so long as balance is maintained between subpopulation extinction, patch migration, and recolonization (Harrison 1991;

Thrall et al. 1998; Freckleton and Watkinson 2002). When the population is well mixed and is not represented as several discontinuous subpopulations, the metapopulation can be described using subjective boundaries to separate patches (Thomas and Kunin 1999).

Habitat Fragmentation

Metapopulation theory often is applied in studies that examine the effects of habitat loss and fragmentation on population dynamics (Opdam 1991; Moilanen and Hanski 1998). Habitat fragmentation is the process in which large continuous areas of native habitat are divided into smaller, disjoint patches (Primack 2002), resulting in a loss of habitat and isolation of surviving patches (Andren 1994). These subpopulations or islands of habitat are any area suitable to sustain a species surrounded by an area of unsuitable habitat (MacArthur and Wilson 1967). There are two pressures that influence the fragmentation of a particular habitat. The first is slow, steady separation that creates an ecological or geographic barrier that blocks further contact (Mayr 1940). Years of constant change allow species to adapt and become genetically diverse, leading to evolutionary changes such as speciation (Mayr 1963; Templeton et al. 2001). A second force leading to habitat fragmentation is human-induced habitat destruction. Human-induced fragmentation includes the destruction of natural habitat (e.g. tropical forest) for the development of cropland, pastures, roads, and settlements (Myers 1988; Lord and Norton 1990; Bierregaard et al. 1992; Gustafson and Gardner 1996; With et al. 1997; Davies et al. 2001). The latter

pressure has been the focus of many ecological studies because it occurs on a much shorter time scale and can be more easily observed and researched than geographical processes (Helliwell 1976; Whitcomb et al. 1981; Howe 1984; Lynch and Whigham 1984; Opdam et al. 1985; Wilcove et al. 1986). Because human influences act so quickly and dramatically on habitats, species may not have time to adapt to the changes. Therefore, this typically leads to reduced population sizes and possibly extinction (Templeton et al. 2001; Fahrig 2002).

Fragmentation can lead to patch isolation, decreases in patch sizes, changes in the interior area:edge ratio, and variations in patch interactions that alter the configuration of animal populations (Noss and Csuti 1997). When a habitat is broken into sections, the flora and fauna are isolated to various extents (Lovejoy et al. 1984; Wilcove et al. 1986). The degree of isolation can affect the dispersal of individuals and, ultimately, the amount of gene flow between subpopulations (Dunphy and Hamrick 2007). For local populations that are severely isolated, decreased ability to attract recruits to the area reduces gene flow and results in an increase in potential for local extinction (Menges and Dolan 1998).

Every species has a minimum patch area that would allow their population to survive. (Haila and Hanski 1984). Even if the total area of a habitat does not change after a fragmentation event(s), the area of each patch can be a more important factor as it determines how many species can live in a fragmented

habitat. Therefore, if the habitat of a species is fragmented into patches below the minimum patch area, extinction will occur (Rosenzweig 1995).

The reduction of habitat due to fragmentation, in effect, creates islands that have higher densities as displaced species are concentrated in the patchy habitat that remains. This results in super-saturation of a significantly smaller area than was previously available (Burgess and Sharpe 1981; Lovejoy et al. 1986; Saunders et al. 1991). A saturated population has a threshold for the maximum number of individuals or species that can coexist without deaths or extinctions occurring (Lee and Bruno 2009). Resource partitioning and competition act to keep populations from exceeding this threshold (MacArthur 1965). As a result of super-saturation, the subpopulation may experience changes in the availability of resources, altered predator-prey interactions, inter- and intra-specific competition, and invasion by introduced species (Saunders et al. 1991). The risk of extinction is higher in subpopulations that are saturated than in those that are not, as they have higher extinction:immigration ratios (He et al. 2005). Hence, it is logical that super-saturation is temporary, as the population cannot remain in this state without experiencing local extinction (Lee and Bruno 2009).

The edge of a habitat can have different properties than the interior and in general, the degree of habitat fragmentation increases the amount of edge (Laurance and Yensen 1991). When fragmentation occurs, it may considerably change the edge and interior characters of the habitat fragments. The effect of

contrasting habitats abutting each other is known as “edge effects”. The amount of edge present and the degree of edge effect will be greater in an area with high fragmentation when compared to areas that are less fragmented. There are systematic differences (such as mating and nesting success, parasitism, predation, food availability, competition, and microclimate) at the edge of a patch compared to the interior that will affect species in diverse ways (Winter and Faaborg 1999). Wiens (1969) found that many species avoid edges, possibly explaining why there are lower densities nearer to habitat edges than away from edges (Helzer and Jelinski 1999). It has been hypothesized that nests found at the interior of a fragment have a higher rate of success than those located at the edge (Johnson and Temple 1986). As seen in Dickcissel (*Spiza americana*), Savannah Sparrows (*Passerculus sandwichensis*), and other grassland and prairie bird species, decreases in the size of a habitat patch negatively influence nesting success (Johnson and Temple 1990; Winter 1999). The degree and type of parasitism differ between the edge and interior of a fragment. Blood parasites (Winter et al. 2000) and brood parasites, such as Brown-headed Cowbirds (*Molothrus ater*) occur at a higher rate in nests that were close (within 50 m) to the edge (Johnson and Temple 1990; Johnson 2001; Jensen and Finck 2004; Patten et al. 2006). Predation and prey availability are two other factors that differ between edge and interior habitats. Nest predation is higher near edges for birds that nest in small prairie fragments (Johnson and Temple 1986, 1990; Burkey 1993; Burger et al. 1994; Robinson et al. 1995; Bollinger and Gavin 2004). Winter et al. (2000) observed an increase in mid-sized carnivore activity

along edges, which could result in prey items remaining confined to the interior of a patch.

In a fragmented habitat, the interspecific competition for the remaining resources can be like a game of “species musical chairs” that leads to an overall decline in population densities (Higgins 2009). The intensity of competition in habitat fragments is much greater than in continuous areas as resident species are less virulent against intruders. If exotics or new species are adapted for the surrounding landscape created by the fragmentation, these native inhabitants often lack biotic resistance or the ability to resist the invasion of the exotic species (Levine et al. 2004; Leigh et al. 2008). Resulting edges distort species interactions within fragments by increasing competition with invasive species and other species already present in the patch (Remer and Head 1998; Anderson and Wait 2001). This can be seen with the invasion of introduced weeds, shrubby vegetation, livestock, and avian species prevalent at newly formed edges (Saunders et al. 1991; Vickery et al. 1994; Hobbs 2001).

In contrast to populations that occupy large continuous habitats, connectivity between local populations in greatly fragmented landscapes is important in order to maintain stability (Noon and McKelvey 1996). Connectivity is the degree to which subpopulations or patches are linked (Dramstad et al. 1996; Tischendorf and Fahrig 2000) and it is described in terms of corridors and matrix properties (Saunders et al. 1991). Corridors (also known as dispersal corridors or landscape linkages) are habitat connections that allow the exchange

of individuals (Beier and Loe 1992). Corridors are a means to reduce negative effects of fragmentation on a habitat (Bond 2003).

In fragmented habitats where edges are created, the area between isolated patches, or the matrix, also plays a role in dispersal of individuals (Russell et al. 2007). The matrix may affect a patch adversely so that dispersal is decreased, the distribution of the species within the patch is reduced, and there is an added reduction in species abundance (Villard et al. 1999). Individuals may choose to forego dispersal or be unsuccessful at dispersing due to the potential of predation, lack of sustainable habitat, and overall risk of mortality associated with the matrix (Russell et al. 2007). The vegetation composition, the structure of the matrix, and the variability in edge effects can all affect subpopulation connectivity (Mesquita et al. 1999).

Fragmentation Effects on Genetics

Fragmentation not only affects the ecology of a species, but the genetics as well. The goal of most population studies is to approximate the amount of genetic variation within and between populations and define the methods that maintain that variation (Nei 1987). Fragmentation affects the rate of gene flow and amount of drift occurring between and within subpopulations. These isolated subpopulations often experience declining population sizes and reduced amounts of gene flow. This is due to extended periods of isolation, which is associated with increased local genetic differentiation between subpopulations, as in the Golden-cheeked Warbler (*Dendroica chrysoparia*) (Lindsay et al. 2008),

and decreased genetic diversity within subpopulations (Mayr 1963; Frankham 1995; Menges and Dolan 1998; Wilson and Provan 2003; Schtickzelle et al. 2006; Dunphy and Hamrick 2007; Dixo et al. 2009). It is expected that genetic differentiation would be highest in subpopulations that are most isolated (Segelbacher et al. 2003). Elevated migration rates and gene flow between subpopulations keep them from diverging and reduces the risk of inbreeding depression (Olivieri et al. 1990; Thrall et al. 1998). However, if no gene flow occurs between isolated subpopulations and they remain genetically separated long enough, there is the potential for speciation (Hewitt 1996, 2001). Issues with measuring gene flow occur when species have low rates of migration because there is no known way to differentiate between species where gene flow is occurring but at low levels and species where no gene flow is occurring at all (Slatkin 1981).

The ability to estimate population differentiation is vital in a metapopulation study because it can help predict how individuals in a population are dispersing. This is then related to the spatial extent of the metapopulation (Storfer 2003). Measures of population differentiation and diversity come from calculations of F-statistics and allele frequencies in natural populations (Wright et al. 1942; Yokoyama 1979; Queller et al. 1993; Storfer 2003). These F-statistics compare the level of heterozygosity among subpopulations to values expected if individuals were randomly mating (Wright 1931; Slatkin 1987).

Of the many genetic markers that are available for use in understanding population structure, microsatellites are ideal because they are relatively easy to use, readily available, and cost efficient. Microsatellites are simple, tandem repeating segments in the DNA; they have a high rate of non-lethal mutations which provide highly variable, scorable loci (Queller et al. 1993; Slatkin 1995). There are a multitude of microsatellite loci for eukaryotes (Tautz and Renz 1984). Genetic differentiation of two squirrel species (*Sciurus niger* and *S. carolinensis*; Moncrief et al. 2008) and the estimation of genetic differentiation among prairie dog colonies (Roach et al. 2001) are only two of hundreds of examples of studies that utilize microsatellites to address population level questions.

Study System

The Lower Rio Grande Valley (LRGV) in the southernmost tip of Texas is one area in the United States severely affected by habitat fragmentation. More than 95% of the native brushland of the LRGV has been destroyed for agricultural and urban development (USFWS 1980, 1985; Parvin 1988). Because of the habitat destruction and subsequent formation of isolated habitat patches, this area provides an ideal site to study metapopulation dynamics.

The Brownsville Common Yellowthroat (*Geothlypis trichas insperata*; Figure 3), a subspecies of the Common Yellowthroat, is affected by the habitat destruction occurring in the LRGV (Vickery et al. 1994). Genetic analysis of the Brownsville subspecies shows a high level of differentiation from other populations sampled across North America (Klicka1994). *G. t. insperata* breeds

FIGURE 3. Typical color patterns seen in male “Brownsville” Common Yellowthroats.

from late March/early April through mid July, with most pairs being established before mid-February (Klicka 1994). Males will defend territories against conspecific males, as will females defend against other females (Hofslund 1959). Estimated territory size is 0.1 ha (Klicka 1994).

Few records are available for Common Yellowthroats in the LRGV which makes determining its current status a challenge. The first recorded description of Brownsville Yellowthroat as a breeding bird in south Texas comes from Fort Brown in 1876 (Merrill1878). It was not until 1930 that they were recognized as a distinct subspecies (Van Tyne 1933). Brownsville Yellowthroat populations have fluctuated over the years due to seasonal climate changes, such as droughts, floods, hurricanes, etc, that have continually affected the population size (Klicka 1994). However, a combination of human modification of the habitat and two major stochastic events may be the reason *G. t. insperata* was considered extinct by the 1950s (Oberholser 1974). There was a considerable amount of habitat

loss, in the late 19th century, when Europeans settled in the region and agriculture became a major industry after railroads were built through Brownsville, Texas (Parvin 1988). Then an extended drought, that dried 20 km of the Rio Grande River, in early 1950's and "the great freeze of 1951" may have lead researchers to believe the subspecies to be extinct (Goldman and Watson 1953; Oberholser 1974).

This subspecies is extremely rare and utilizes habitat that has been severely contracted. In 1988, Klicka (1994) estimated between 100 to 150 breeding pairs of Brownsville Yellowthroat to exist along the Rio Grande River. And since the last study on this subspecies (by Klicka 1988-1989), a severe drought in 1988 and a hard freeze in 1990 afflicted this area. These events possibly reduced the population size further. Klicka also estimated an apparent survivorship of 55% after two years of data collection. His estimates were a rough measurement based on the number of individuals he had recaptured from one year to the next. He often found Brownsville Yellowthroats in isolated riparian habitats surrounded by croplands. A riparian zone includes the habitat found in the transition interface between land and a body of water, such as a pond or a river. Several factors may explain why *G. t. insperata* densities are low. Factors include seasonal draining and flooding of natural water reservoirs and marshes, cowbird (*Molothrus ater* and *M. aeneus*) parasitism, overgrazing of natural habitat by livestock, and the mowing and burning of preferred habitat (Klicka 1994).

One possible explanation for the lack of consistency and shortage of *G. t. insperata* records in the LRGV could be associated with ecotourism. The LRGV is a unique junction of temperate and tropical zones in the U.S. Therefore, the biodiversity is quite high and ecotourism is an ever increasing portion of the travel market and one of the fastest growing tourisms markets. Outdoor activities are available for all types of enthusiasts, but birding (e.g. watching, photography, etc.) is a main attraction. Over 75% of the bird species found in the U.S. can be seen in the state of Texas (Mathis and Matisoff 2004). Texas is internationally known for having three of the top 12 "birding hot spots" with the LRGV being the sixth best site for birding in North America (Konrad 1996). For many bird watchers, this area is prime location for those bird species migrating to Central and South America. The continent forms a natural bottleneck or funnel at the base of Texas, where a high density and variety of birds can be seen during migration. Many birders prefer to visit during the mild winters of south Texas (as opposed to the hot, humid summers) to find species such as the Sandhill Crane (*Grus canadensis*), Peregrine Falcon (*Falco peregrinus*), and Piping Plover (*Charadrius melodus*) in addition to around 40 species whose range barely extends north to this region (USFWS 2002). There are an estimated 125,000 "Winter Texans" in the Texas Rio Grande Valley, with 40-50% of those visiting wildlife reserves while in Texas (Vincent et al. 2003). Rare breeding records for the Common Yellowthroat could be due to the lack of a summer birding "hot spot" in the LRGV.

The subspecies is recognized as breeding in the southern tip of Texas and is found in the Rio Grande Delta below Brownsville, Texas (Brewster 1883; Wolfe 1956). Oberholser (1974) noted their range to be restricted to Cameron, Willacy, Hidalgo, and Starr counties in Texas (Figures 4 and 5). Currently, the Brownsville Yellowthroat is thought to be limited to the southernmost regions of Cameron County, Texas and possibly in the adjacent region of north Tamaulipas, Mexico (Figures 4 and 6; Klicka 1994; Dunn and Garrett 1997). *Geothlypis trichas* breeds south into Tamaulipas, Mexico; however, taxonomic study indicates these are not of the *G. t. insperata* subspecies (Klicka 1994). Literature regarding their wintering range was largely inconclusive. Before 1994, their wintering status was unclear; where Van Tyne (1933) and Gross (1953) assumed that the subspecies left south Texas for the winter. Later, Oberholser (1974) suggested they were partial residents, but the American Ornithologists' Union (1957) and Klicka (1994) considered them permanent, year-round, residents.

Klicka (1994) determined that the Brownsville Yellowthroat population was highly sedentary and noted that males, females, and young of the year were present throughout the year. Males and females also will actively exclude migrant Common Yellowthroats from territories during migration (Klicka 1994). Males defend the same territory all year except during a brief period when fall molt occurs. Interestingly, boundaries between neighboring territories are more relaxed during the period when pairs feed nestlings and while fledglings are still present (Hofslung 1959; Klicka 1994).

FIGURE 4. The approximate breeding distributions of the 12 Common Yellowthroat subspecies recognized by the American Ornithologists' Union (AOU 1957). The distribution map was produced by Klicka (1994) based on written geographic descriptions.

FIGURE 5. Four Common Yellowthroat subspecies have breeding distributions that extend partially into the state of Texas. These limits were illustrated by Klicka (1994) based on written descriptions by Oberholser (1974).

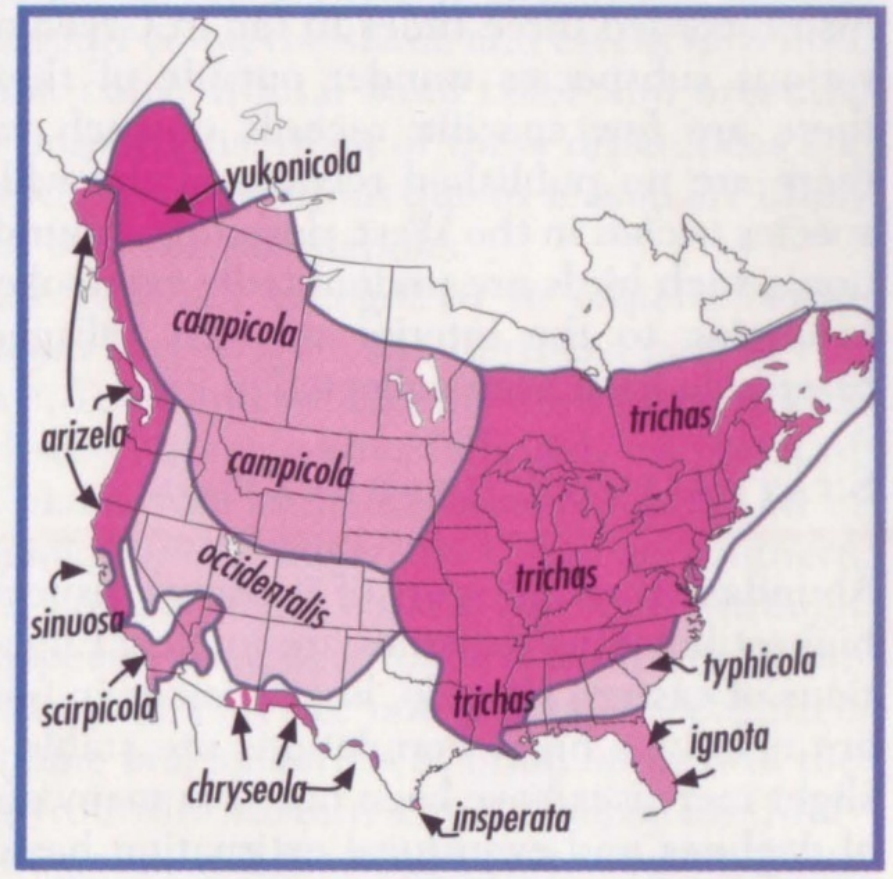

FIGURE 6. Map of the United States and a portion of Canada representing the distribution of each Common Yellowthroat subspecies (Dunn and Garrett 1997)

Old oxbow lakes or “resacas” (a regional term) are isolated water reservoirs that are flooded most of the year except during dry periods during summer months (Brush 2005). During periods of drought, territories can be found in resaca bottoms that may range from damp to completely dry. These resacas typically are surrounded by agricultural plots or some other form of unsuitable habitat. The dominant vegetation found within *G. t. insperata*

territories varies slightly from one location to another and habitats of known *G. t. insperata* territories tend to share a common vegetation structure (Klicka 1994). During the breeding season, *G. t. insperata* is found in reeds (*Arundo donax* and *Phragmites australis*), Southern Cattail (*Typha domingensis*), baccharis (*Baccharis neglecta, B. salicifolia, B. texana*), and willows (*Salix exigua and S. nigra*) (Klicka 1994; Dunn and Garrett 1997; Brush 2005).

At this time, density of wetlands in the LRGV decreases north from the Rio Grande River and becomes more scattered in northern Cameron and Hidalgo Counties (Figure 7; TPWD 1997). Brownsville Yellowthroats utilize these wetlands and their territories are predominantly located around the perimeter of resacas or along the bank of the Rio Grande River. With suitable habitat found frequently along or near the Rio Grande River, this habitat should allow ample gene flow throughout the most southern area. The habitat along the shore of the River now resembles a highway, of sorts, for individuals to migrate locally east and west. Suitable habitat is more intermittent away from the River, especially at the northern boundaries of the Brownsville Yellowthroat's distribution. Consequently, gene flow should be less continuous throughout these more northern areas.

G. t. insperata is an excellent organism to apply metapopulation theory and study the effects of human activity and habitat fragmentation, because it lives in such well-delimited habitat patches along the Rio Grande River and around the banks of resacas or water reservoirs. It is not clearly understood how

habitat fragmentation has affected this subspecies and the amount of gene flow between neighboring habitat patches is unknown. Such information will help determine if this subspecies is of conservation concern and provide support for the development of conservation techniques to ensure its survival. Green (2005) states that one part of conservation biology is the identification of natural populations that ought to be protected; and in efforts to conserve and protect diversity, populations below the species level should be considered when applicable.

Hypotheses

1. Apparent survivorship of Brownsville Yellowthroats in the LRGV has not changed since the 1988-1989 study conducted by Klicka (1994).

2. The size of an individual male's territory was difficult to determine and did not appear to be consistent among habitat types (River versus resaca). Therefore, linear density was used in lieu of area density. Considering that wetlands are more concentrated along the Rio Grande River, linear density of Brownsville Yellowthroats is greatest nearer to the River.

3. Since this suitable riparian habitat for *G. t. insperata* becomes more dispersed south to north, I expect individuals on or near the Rio Grande River will be more closely related than northern individuals.

4. The source-sink metapopulation model should be the model best fit to describe this subspecies.

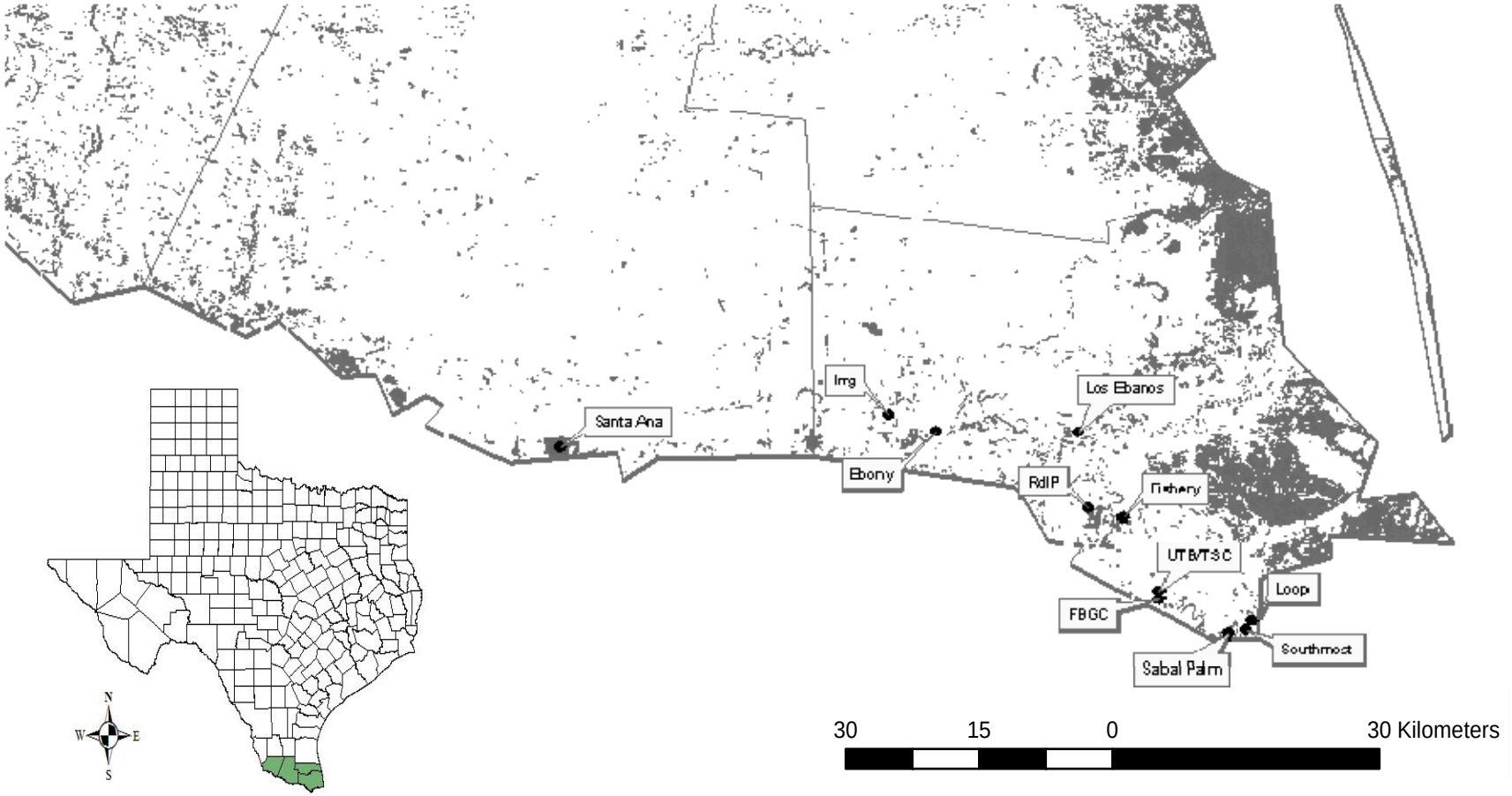

FIGURE 7. The distribution of wetlands (shown in dark gray) in Cameron, Willacy, Hidalgo, and Starr Counties, Texas (Geospatial Data Gateway). Individuals were banded and DNA samples were taken from 11 sites in Cameron and Hidalgo Counties.

II. METHODS

Field Methods

I conducted field research, including mist-netting, banding, and collecting blood samples, during the months of May-July 2008 and May-August 2009 in the Lower Rio Grande Valley of south Texas. Samples were taken from ten sites in Cameron County and one site in Hidalgo County (Figure 7). No samples were taken from Willacy and Starr counties because no known populations reside in these counties (Klicka 1994).

Male Brownsville Yellowthroats were located using a combination of point count data and plot searching. Point counts rely on visual and aural recognition to identify species present in a sampling area and are useful in studying avian population trends (Bibby et al. 2000). Plot searching involves searching potentially suitable habitat for an individual of a particular species who is defending a territory (Bibby et al. 2000). Interviews with Texas wildlife officers, other researchers, and private land-owners provided additional information about possible Brownsville Yellowthroat locations.

I used a targeted and active trapping system. Once a Brownsville Yellowthroat was confirmed in the vicinity, I listened for general direction and distance of their song and used a Common Yellowthroat call playback recording in order to elicit a response. Because Brownsville Yellowthroats distribute their territories linearly along the banks of the Rio Grande River and around resacas, I

was able to rapidly locate several sequential territories over a short period of time.

The perimeter of an individual male's territory was roughly estimated using the recording. From there, a mist net (6 m x 2.6 m, 24 mm mesh size) was erected in suitable habitat near the suspected center of the defended territory. A hand-painted decoy (Figure 8), mimicking male Common Yellowthroat color patterns, and a male song/call playback were used in conjunction with the mist

FIGURE 8. Male Brownsville Yellowthroat (left) seen with partially painted decoy (right).

net. I used a recording to broadcast the presence of a trespasser in the territory. The decoy and recording were set up 1.0-1.5 m off the ground and centered on the opposite side of the net that the defending male would predictably attack (Figure 9). The recording was initially used to attract a male from afar. Then the decoy and recording, posed as an intruder, attracted that male toward the decoy

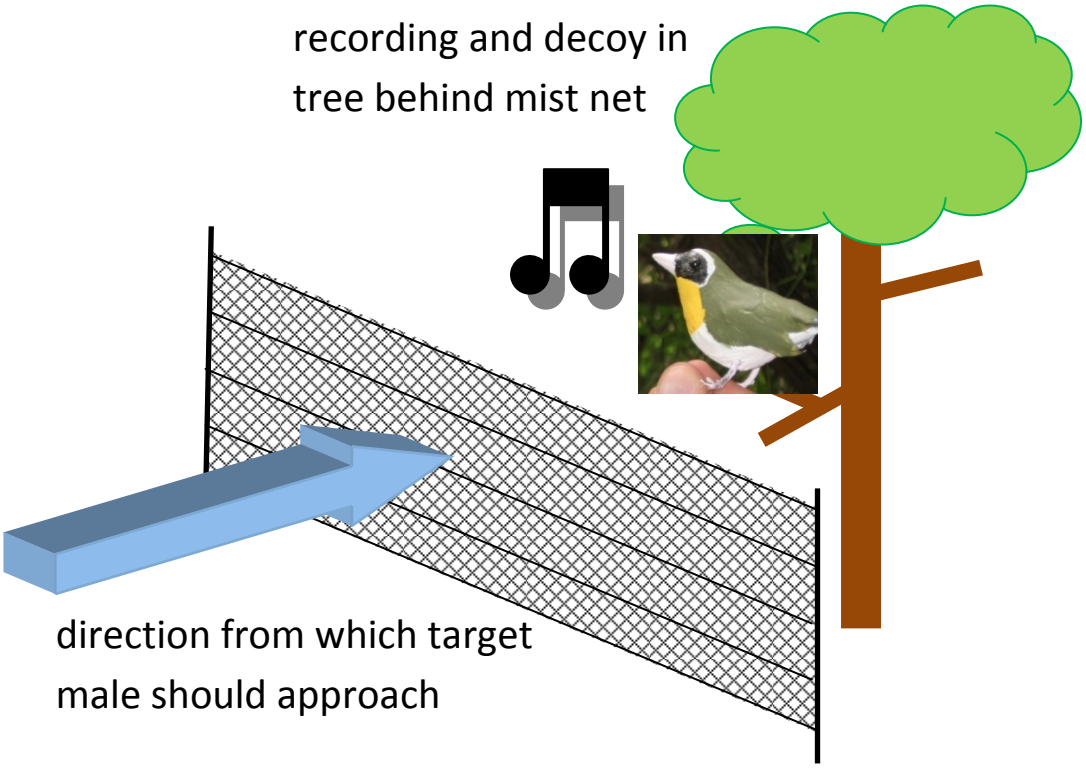

FIGURE 9. Diagram depicting a typical set-up of a mist net, Common Yellowthroat decoy, and Common Yellowthroat recordings. Recordings elicited a defense response from the target male that flew into the mist net before encountering the decoy.

and into the net. The decoy and recording were set up behind the net in order to entangle the defending male before he encountered the decoy. The Common Yellowthroat calls and songs were played in a continuous loop for no longer than 30 minutes. This time limit was subjective based on personal observation; after 30 minutes of playbacks without a successful capture, defending males appeared to lose interest and became impassive. This was rarely an issue since nearly all trapping attempts were successful in this allotted time. However, if not successful, additional attempts were made on a later day (no earlier than seven days as to not desensitize the defending male to my recordings). Male Brownsville Yellowthroats are extremely responsive to playback recordings. Thus, the probability of overlooking a territorial male in a particular study area was very low (Klicka 1994). Males were the targeted sex because they were the least labor-intensive to locate and capture, but all females, juveniles, and nestlings that I captured also were banded and processed.

As previously stated, the linear fashion in which males form territories along the water's edge allowed me to locate and capture several males over a short stretch of river and a small area around resacas. Although males were relatively easy to locate, not all individuals I encountered were netted due to several possible circumstances. Many times a male's territory was inaccessible because terrain or vegetation made the area impassible. Another reason located males were not captured was attributed to the age of the target. There were cases where hatch-year (HY) or possibly inferior after hatch-year (AHY) individuals responded to my recordings but did not defend a territory as

vigorously as would be expected by an older male. In this situation, I suspect that recordings elicited a “flight” rather than “fight” response from these males.

Captured individuals were banded with a federal aluminum metal band containing a unique serial number issued by the USGS Bird Banding Laboratory. Body measurements taken were mass, using a digital scale (measured to the nearest 0.1 g), and wing chord, using a stopped wing rule (measured to the nearest mm). When circumstances permitted, additional data on juvenile Brownsville Yellowthroats were gathered describing plumage and molt limits. Tail length for some unsexed individuals was taken to assist in sex determination. Because many juvenile males markedly resemble juvenile and adult females, tail length is a known morphological indicator of sex.

Blood samples were collected from each captured Brownsville Yellowthroat individual based on methods described by Thusius et al. (2001). The ulna vein, located on the ventral side of the wing proximal to the body, was pricked with a sterile 30 gauge syringe. Blood was collected using a 5 µL micro-capillary tube as prescribed by the Ornithological Council (1999). The Ornithological Council (1999) suggests a total volume no greater than 5 µL be abstracted from each individual given the mass of the Brownsville Yellowthroat. However, only 1 µL was taken from several individuals due to concerns about their well-being. The blood was then expelled from the capillary tube into a vial of lysis storage buffer (50 mL of 2M Tris [pH8.0], 200 mL of 0.5M EDTA, 2 mL of 5M NaCl, 50 mL of 10% SDS, 698 mL of ddH_2O) to prevent coagulation and

preserve the integrity of the DNA. Each vial contained pertinent information about the sample including the individual's unique band identification number, capture date, and sample number. The vial was then stored at room temperature.

Laboratory Methods

Whole genomic DNA was isolated from the blood/lysis buffer solution following the spin-column protocol for "Purification of total DNA from animal blood" as a part of the DNeasy Blood and Tissue Kit (Qiagen, Valencia, California; specific protocol provided by manufacturer). Following extraction, purified DNA was stored at 4ºC.

To examine genetic variation among sampled individuals for specific microsatellite DNA loci, polymerase chain reactions (PCR) were run using 14 single copy loci and one multi-copy locus (VeCr14) (Table 1). To date, no microsatellite loci have been isolated or characterized for the Common Yellowthroat. Therefore, I used loci developed for three species that are closely related, taxonomically, to the Common Yellowthroat. These include the Yellow Warbler (*Dendroica petechia*), Black-throated Blue Warbler (*D. caerulescens*), and Golden-winged Warbler (*Vermivora chrysoptera*) (Table 1; Dawson et al. 1997; Webster et al. 2001; Stenzler et al. 2004). The primers described in these papers are known to amplify Common Yellowthroats microsatellites.

TABLE 1. The name, repeat motif, and sequence of all the primers used in this research. Not all primers were successfully run through the genetic analyzer. Four primers successfully amplified through PCR but were not successfully analyzed through the sequencer. Two primers could not be amplified.

Primer Name	Repeat Motif	Primer Sequence	Top Level of Success
*Dpu*01[a]	$(CA)_{22}$	F: GGATTCACACCCCAAAATT R: AGAAGTATATAGTGCCGCTTGC	Genotyping
*Dpu*16[a]	$(AC)_{12}(GC)_4A$ CGCAC$(GC)_2$	F: ACAGCAAGGTCAGAATTAAA R: AACTGTTGTGTCTGAGCCT	None
*Dca*24[b]	N/A	F: TGGGAGCCAGGAGAAGTTGTTTG R: CGGGGATCNTCTGTAGGTCGAAT	None
*Dca*28[b]	N/A	F: CTTCACAACCACAGTAAACC R: CAAATTCTTGCAGTCATAGC	Genotyping
*VeCr*01[c]	$(CTT)_2CCTT($ ATC$)_4$	F: ATTGGAGACCTCATCTGCGTTTT R: TGGGAACATATACTGTGCTGAAGG	Genotyping
*VeCr*02[c]	$(TCA)_7$	F: AATAGGCTTTGAGGAGGAATCC R: AGCCCCAAAGTGCTGAAATA	Genotyping
*VeCr*03[c]	$(GTT)_6$	F: GGCACTTGACAGCAGCAGAGATG R: CTTGGGGTGTCCCTAAACAGTCAT	PCR
*VeCr*04[c]	$(CAT)_9$	F: TGCAGGGATGTTGTGACCA R: TGTCTCCTGTACCCTGCAC	PCR
*VeCr*05[c]	$(AC)_8$	F: ACACACTTATGTGCATGGGCT R: ATATTTCAGGTATGGGTTTGGTTC	PCR
*VeCr*06[c]	$(ATG)_3TTG(A$ TG$)_3$	F: TGTCCTCCCCCTGTTTGTTTTA R: ATTGTCCCCACTGCATCCTTCA	Genotyping
*VeCr*07[c]	$(CA)_9$	F: CTCGGTATGTGTCCCTGCCTTA R: TTATTCCCTGCAGTTGCTGTGA	Genotyping
*VeCr*10[c]	$(TTC)_6$	F: CATATACGTGCACCCTCTTCAT R: TGAGCATTCCTGGTTTCAGATA	PCR
*VeCr*11[c]	$(CAA)_6$	F: GGGAGCCCATTTGGATGTTTCA R: GTGGCTGCACACCCCTACAGTG	Genotyping
**VeCr*14[c]	$(ATG)_{13}$	F: GTTATACCTGCGTGAGTGT R: AGCCTTGTTATCCTTCTTC	Genotyping
*VeCr*16[c]	$(CAA)_5$ . . . $(CAA)_4$	F: TAAAACTTCCCTGCAATAACCT R: GCCGATGTAGACAAAGAAAG	Genotyping

A Dawson et al. 1997
B Webster et al. 2001
C Stenzler et al. 2004

* *VeCr*14 is multicopy locus

PCR master mix ingredients and their respective concentrations (Table 2) and the corresponding profiles (Table 3) varied between the primers used. All reactions ran in 25 µL total volumes. The amplified PCR product was analyzed using an Applied Biosystems 3130 Genetic Analyzer (Applied Biosystems Inc., Foster City, California) in a reaction of 13 µL of Hi-Di Formamide, 1 µL ROX size standard, and 1 µL PCR product. In conjunction with the analyzer, GENEMAPPER v 4.0 (Applied Biosystems Inc.) software was used to provide sizing and quality allele calls (i.e. scores).

Statistical Method

Genotypes from the analyzed loci were input into the program STRUCTURE (Pritchard et al. 2000) in order to predict population structure, identify the presence of distinct subpopulations, and assign individuals into those subpopulations. A series of burnin and Markov chain Monte Carlo (MCMC) iterations were used to test the data. The most consistent estimates of population structure resulted from a burnin of 100,000 followed by 1,000,000 MCMC iterations. These parameters were used to test the probability of sampled individuals representing one, two, three, four, or five subpopulations.

CERVUS (Marshall et al. 1998; Kalinowski et al. 2007) was used to estimate allele frequencies. GENEPOP (http://genepop.curtin.edu.au/; Raymond and Rousset 1995; Rousset 2008) was used to perform the Hardy-Weinberg Exact Test, Linkage Disequilibrium, and Population Differentiation tests, as well as obtain basic information (i.e. observed and expected number of homozygotes

TABLE 2. Master mix (µL/rxn) used for each primer. Each primer required a specific master mix in order to achieve proper amplification during polymerase chain reactions. These master mixes may differ from those described by the developing researchers; some alterations were necessary to maximize PCR products.

Primer	Buffer	dNTP	Forward Primer	Reverse Primer	*Taq* polymerase	H_2O	$MgCl_2$	DNA	Total µL
*Dpu*01	2.5	2.5	1	1	0.2	9.8	6	2	25
*Dpu*16	2.5	2.5	1	1	0.2	13.8	2	2	25
*Dca*24	2.5	2.5	1	1	0.2	9.8	6	2	25
*Dca*28	2.5	2.5	1	1	0.2	9.8	6	2	25
*VeCr*01	2.5	2.5	1	1	0.2	13.8	2	2	25
*VeCr*02	2.5	2.5	1	1	0.2	13.8	2	2	25
*VeCr*03	2.5	2.5	1	1	0.2	8.8	8	1	25
*VeCr*04	2.5	2.5	1	1	0.2	10.8	6	1	25
*VeCr*05	2.5	2.5	1	1	0.2	10.8	6	1	25
*VeCr*06	2.5	2.5	1	1	0.2	13.8	2	2	25
*VeCr*07	2.5	2.5	1	1	0.2	11.8	4	2	25
*VeCr*10	2.5	2.5	1	1	0.2	8.8	6	3	25
*VeCr*11	2.5	2.5	1	1	0.2	13.8	2	2	25
*VeCr*14	2.5	2.5	1	1	0.2	13.8	2	2	25
*VeCr*16	2.5	2.5	1	1	0.2	13.8	2	2	25

TABLE 3. Primers developed from different species require specific profiles to allow proper amplification during polymerase chain reactions. Those specifications are presented below.

Primer	Initialization	Denaturation	Annealing	Elongation	# of Repeats	Final Elongation	Final Hold
*Dpu*01	94˚C-3 min	[94˚C-3 min	52˚C-30 sec	72˚C-1 min]	x 30	72˚C-10 min	10˚C-∞
*Dpu*16	94˚C-3 min	[94˚C-3 min	52˚C-30 sec	72˚C-1 min]	x 30	72˚C-10 min	10˚C-∞
*Dca*24	94˚C-3 min	[94˚C-3 min	52˚C-30 sec	72˚C-1 min]	x 29	72˚C-10 min	10˚C-∞
*Dca*28	94˚C-3 min	[94˚C-3 min	52˚C-30 sec	72˚C-1 min]	x 30	72˚C-10 min	10˚C-∞
*VeCr*01	94˚C-3 min	[94˚C-3 min	51˚C-30 sec	72˚C-1 min]	x 30	72˚C-10 min	10˚C-∞
*VeCr*02	94˚C-3 min	[94˚C-3 min	51˚C-30 sec	72˚C-1 min]	x 30	72˚C-10 min	10˚C-∞
*VeCr*03	94˚C-3 min	[94˚C-3 min	52˚C-30 sec	72˚C-1 min]	x 30	72˚C-10 min	10˚C-∞
*VeCr*04	94˚C-3 min	[94˚C-3 min	52˚C-30 sec	72˚C-1 min]	x 30	72˚C-10 min	10˚C-∞
*VeCr*05	94˚C-3 min	[94˚C-3 min	52˚C-30 sec	72˚C-1 min]	x 30	72˚C-10 min	10˚C-∞
*VeCr*06	94˚C-3 min	[94˚C-3 min	51˚C-30 sec	72˚C-1 min]	x 30	72˚C-10 min	10˚C-∞
*VeCr*07	94˚C-3 min	[94˚C-3 min	51˚C-30 sec	72˚C-1 min]	x 30	72˚C-10 min	10˚C-∞
*VeCr*10	94˚C-3 min	[94˚C-3 min	52˚C-30 sec	72˚C-1 min]	x 30	72˚C-10 min	10˚C-∞
*VeCr*11	94˚C-3 min	[94˚C-3 min	51˚C-30 sec	72˚C-1 min]	x 30	72˚C-10 min	10˚C-∞
*VeCr*14	94˚C-3 min	[94˚C-3 min	51˚C-30 sec	72˚C-1 min]	x 30	72˚C-10 min	10˚C-∞
*VeCr*16	94˚C-3 min	[94˚C-3 min	51˚C-30 sec	72˚C-1 min]	x 30	72˚C-10 min	10˚C-∞

and heterozygotes, and allele frequencies). For Hardy-Weinberg Exact Tests, a probability test for each locus with no complete enumeration of alleles and the default Markov chain parameters was used. Linkage disequilibrium analyzes diploid data to test for disequilibrium among each pair of loci in each population. Tests were performed using probability tests and the default Markov chain parameters. Population differentiation, including genic and genotypic, was assessed for all populations with the default Markov chain parameters.

RELATEDNESS is a software application used to estimate the average genetic relatedness among sets of individuals (http://gsoftnet.us/GSoft.html; Queller and Goodnight 1989; Goodnight and Queller 1995). Genotypes were entered into the program to compute pairwise relatedness values and average relatedness values for the total population.

A Mann-Whitney test was performed on linear density using R 2.10 software (R Development Core Team 2008). Results were presented as mean ± standard error.

III. RESULTS

Brownsville Yellowthroats (n = 128) were sampled from May to August in 2008 (n = 77) and 2009 (n = 51). In 2008, I banded 71 males and six females (Table 4); three individuals were juveniles/nestlings who required the use of DNA sexing techniques because they were too young to reliably sex in the field. Of these individuals sampled in 2008, I recaptured three males through the course of the 2008 field season and sampled one male previously banded 29 July 2006 by Christopher Butler. In 2009, 46 males and five females were sampled (Table 4); five individuals were juvenile/nestlings. During the 2009 field season, I attempted to recapture Brownsville Yellowthroats from the same area they were banded during 2008. All Brownsville Yellowthroats recaptured in the 2009 field season were males (n = 26). Most, but not all, appeared to defend the same territory in which they originally were captured in 2008. Recaptured individuals not defending the same territory were netted in the near vicinity (0.168 ± 0.061 km) of the 2008 capture locality (Table 5).

Linear density was estimated for both banded individuals and total encountered individuals for 2008 and 2009. The linear density for banded Brownsville Yellowthroats in 2008 and 2009 was 3.09 ± 0.74 individuals/km and 1.05 ± 0.44 individuals/km, respectively. The linear density of all encountered individuals in 2008 and 2009 was 4.62 ± 0.98 individuals/km and 3.56 ± 0.77 individuals/km, respectively. The linear density of banded Brownsville Yellowthroats was examined and compared between sites close (i.e. < 2 km) to

TABLE 4. The number of male and female Brownsville Yellowthroats captured at each of the sample sites visited. Lat/Long coordinates for each site are presented. Sample size values represent new captures.

Sample Site	Sample Size		Coordinates	
	Male	Female	N	W
Nature Conservancy in Texas-Lennox Foundation Southmost Preserve	2008: 32 2009: 15	2008: 4 2009: 1	25˚ 51' 15.39"	97˚ 23' 51.7524"
Sabal Palm Audubon Center	2008: 7 2009: 1	2008: 1 2009: 0	25˚ 51' 3.2976"	97˚ 25' 1.7574"
The University of Texas at Brownsville and Texas Southmost College	2008: 4 2009: 1	2008: 0 2009: 0	25˚ 54' 0.0606"	97˚ 29' 30.9294"
Santa Ana National Wildlife Refuge	2008: 0 2009: 8	2008: 0 2009: 2	26˚ 4' 15.0744"	98˚ 8' 43.5048"
Los Ebanos Preserve	2008: 7 2009: 1	2008: 0 2009: 0	26˚ 54' 2.22"	97˚ 34' 41.736"
Fort Brown Golf Course	2008: 0 2009: 9	2008: 0 2009: 0	25˚ 53' 25.0650"	97˚ 29' 30.1848"
Resaca de la Palma State Park (RdlP)	2008: 0 2009: 2	2008: 0 2009: 0	25˚ 59' 48.4506"	97˚ 34' 7.5822"
Coastal Fisheries (Texas Department of Parks and Wildlife, Brownsville Field Station)	2008: 4 2009: 1	2008: 0 2009: 1	25˚ 59' 8.8188"	97˚ 31' 50.1954"
Charles Loop property	2008: 17 2009: 0	2008: 1 2009: 0	25˚ 51' 43.0914"	97˚ 22' 17.6226"
Irrigation Reservoir	2008: 0 2009: 4	2008: 0 2009: 0	26˚ 6' 6.1986"	97˚ 47' 3.5808"
Ebony Unit	2008: 0 2009: 4	2008: 0 2009: 1	26˚ 5' 9.8118"	97˚ 44' 31.0956"
TOTAL	2008: 71 2009: 46	2008: 6 2009: 5		

TABLE 5. Twenty-six individuals banded in 2008 were recaptured in 2009. Netting location, the band number for recaptured individuals, along with the direction and distance between 2008 and 2009 capture locations are shown.

Location	Band #	Direction from 2008 to 2009 position	Difference between locations of recaptured ind (m)
Los Ebanos	205011220	-	0
Los Ebanos	205011222	SE	108.207
Fish Hatchery	205011246	-	0
Fish Hatchery	205011247	-	0
Loop (S)	205011249	SSW	35.362
Loop (S)	205011256	NW	84.838
Loop (S)	205011264	ESE	520.564
Sabal Palm	205011216	-	0
Sabal Palm	205011217	-	0
Sabal Palm	205011219	-	0
Sabal Palm	205011223	N	327.049
Southmost	205011204	-	0
Southmost	205011208	-	0
Southmost	205011224	-	0
Southmost	205011225	ENE	188.883
Southmost	205011227	-	0
Southmost	205011228	-	0
Southmost	205011229	SW	43.186
Southmost	205011230	-	0
Southmost	205011231	-	0
Southmost	205011235	-	0
Southmost	205011236	NNE	34.391
Southmost	205011275	-	0
Southmost	205011277	-	0
UTBR	205011272	-	0
UTBR	205011274	-	0

the Rio Grande River and sites far (i.e. > 2 km) from the River. No significant differences were found between near and distant sites for banded Brownsville Yellowthroats in 2008 (W = 47.5, p = 0.5152) or 2009 (W = 16, p = 0.9307). Likewise, near and distant sites for all encountered Brownsville Yellowthroats were not significantly different in either 2008 (W = 3, p = 0.1167) or 2009 (W = 14, p = 0.6389).

Of the 15 microsatellites loci examined (Table 1), I was only able to score allele sizes for nine. Six loci, *Dpu*16 (isolated from Yellow Warblers), *Dca*24 (isolated from Black-throated Blue Warblers), and four from Golden-winged Warbler (*VeCr*03, *VeCr*04, *VeCr*05, *VeCr*10) did not amplify and therefore were not applicable to the Brownsville Yellowthroat. The remaining nine microsatellites amplified correctly; however, three (VeCr01, VeCr06, and VeCr16) appeared to be fixed for all individuals, rendering them less useful for this particular study. One locus (*VeCr*14) amplified two distinct fragments and was determined to be a multi-copy locus. The following results are based on analyses of five single copy loci and one multi-copy locus (seven scorable loci).

Using STRUCTURE, one (K = 1) population was predicted as the most likely to occur in this system (Figure 10). The next most likely situation is the presence of two subpopulations. These predictions were made based on a likelihood value (L(K)) averaged over eight iterations and remain the same whether or not prior knowledge of capture location was provided. The population was in or near Hardy-Weinberg Equilibrium as the mean number of observed

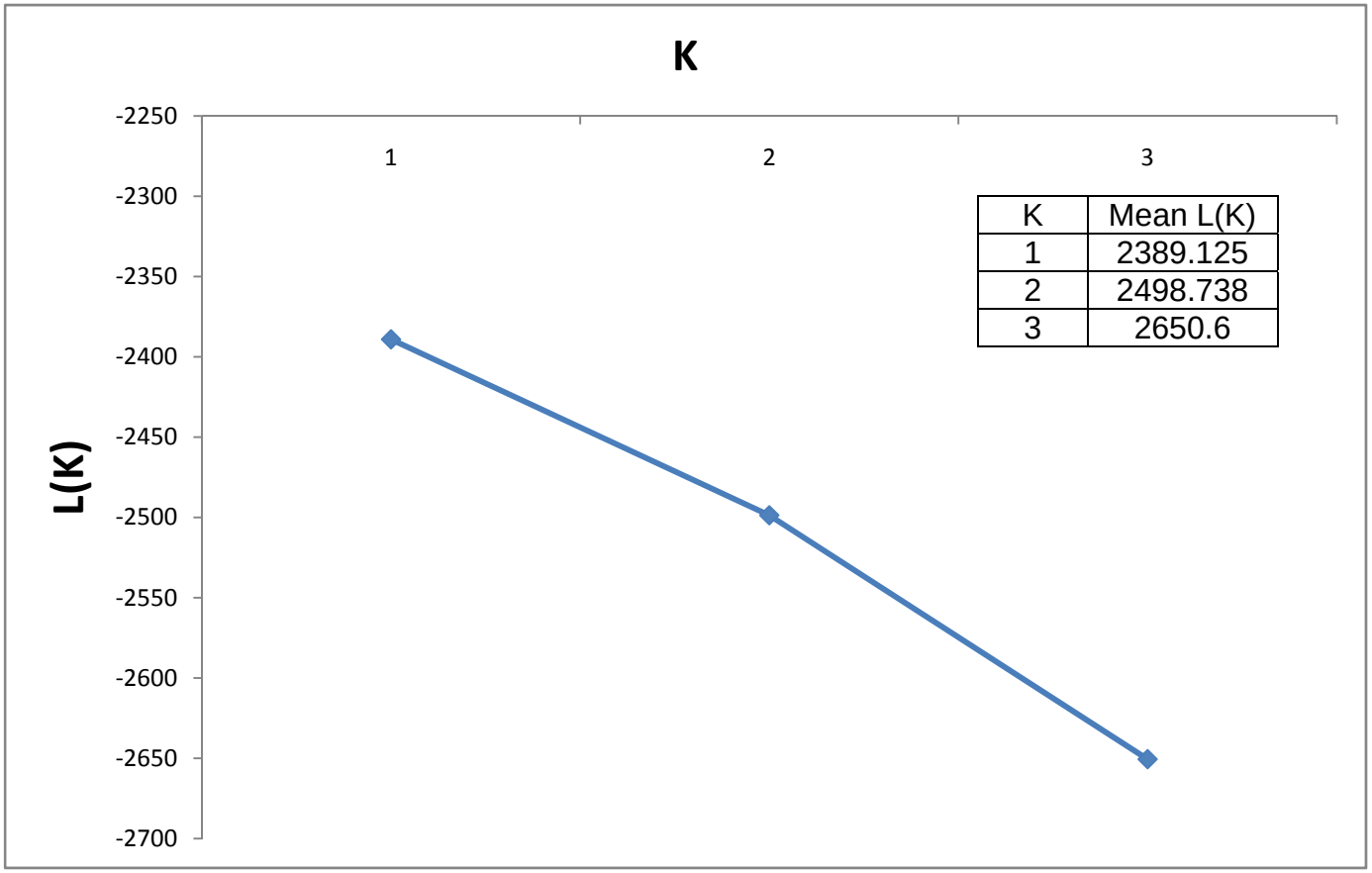

FIGURE 10. The mean calculated likelihood values (L(K)), using STRUCTURE, for the presence of one, two, or three subpopulations (K). The graph indicates that one population is the more likely scenario.

heterozygotes (0.65) was nearly equal to the mean expected number of heterozygotes (0.66), estimated using CERVUS (Table 6). The polymorphic information content, which measures the informativeness of a particular set of genetic markers, was 0.61 (Table 6). Results of genotypic linkage disequilibrium tests, using GENEPOP, showed only five of the possible 21 linkage pairs of loci rejected the null hypothesis that genotypes at one locus are independent from genotypes at the other locus (Table 7); all other pairs failed to reject the null hypothesis. Hardy-Weinberg test results for the entire population are in Table 8.

Estimated relatedness values were organized into the following order as a means of distinguishing levels of relatedness among individuals. Values greater than or equal to 0.4 (1^{st} order) would be comparable to the degree of relatedness shared between full siblings or parent-offspring; values between 0.2 and 0.399 (2^{nd} order) were comparable to half-siblings, aunt/uncle-niece/nephew, or grandparent-grandchild; values between 0.1 and 0.199 (3^{rd} order) were comparable to cousins or great grandparent-great grandchild; values between 0 and 0.099 were considered distant relatives; and values below 0 indicated that one individual is as related to another as any two random individuals chosen from the population. The relatedness value for the entire population was 0.0553.

TABLE 6. CERVUS output for the seven scorable loci. Mean values are calculated over all loci. (PIC = polymorphic information content)

Locus	Observed Heterozygosity	Expected Heterozygosity	PIC
*Dpu*01	0.6	0.83	0.81
*Dca*28	0.75	0.55	0.49
*VeCr*02	0.65	0.65	0.59
*VeCr*07	0.93	0.89	0.87
*VeCr*11	0.39	0.46	0.37
*VeCr*14A	0.4	0.43	0.34
*VeCr*14B	0.81	0.81	0.78
Mean	**0.65**	**0.66**	**0.61**

TABLE 7. Results from genotypic linkage disequilibrium tests show five pairs of loci have genotypes that are not independent from one another.

Locus #1	Locus #2	P-value ± standard error
*Dpu*01	*VeCr*07	0.0077 ± 0.0055
*Dpu*01	*VeCr*14A	0.0473 ± 0.0088
*VeCr*02	*VeCr*14A	0.0377 ± 0.0041
*VeCr*14A	*VeCr*14B	0.0217 ± 0.004
*Dpu*01	*VeCr*02	0.0188 ± 0.0084

TABLE 8. Hardy-Weinberg test results show the p-value ± standard error for each locus in the population.

Locus	P-value ± standard error
*Dpu*01	0.0006 ± 0.0006
*Dca*28	0.0306 ± 0.0020
VeCr02	0.7419 ± 0.0137
VeCr07	0.5462 ± 0.0205
VeCr11	0.1221 ± 0.0052
VeCr14A	0.1746 ± 0.0026
*VeCr*14B	0.5774 ± 0.0157

IV. DISCUSSION

Apparent Survivorship

The apparent survivorship of Brownsville Yellowthroats in the LRGV has not changed in 20 years since the 1988-1989 study conducted by Klicka (1994). Over two field seasons in 2008 and 2009, I banded 128 individuals; 117 of which were males and 11 of which were females (Table 4). I encountered/identified an additional 49 individuals over both seasons; all, but one, were confirmed as male by visual contact or vocal recognition. An “encountered” individual was one seen or heard who could not be captured during the study. Considering all those individuals encountered during this study, I feel as though I sampled a reasonable portion of the population which Klicka (1994) estimated to be around 280 individuals. Regardless of that assumption, at this time I will make no estimation of population size based on these data that have been collected.

There are only a couple estimates of survivorship for the Brownsville Yellowthroat and they differ in their method of estimating survivorship. The Monitoring Avian Productivity and Survivorship (MAPS) Program give two separate demographic parameters that are estimated using several years of data and provide two entirely different probabilities. The survival rate and recapture probability, provided for Common Yellowthroats in the south-central region of the U.S., are estimated to be 0.453 ± 0.041 and 0.468 ± 0.064, respectively (IBP 2010). Survival rate, as defined by MAPS, is the probability of an adult surviving to and returning in a particular year to the area where it was present during the

previous year. In contrast, recapture probability is the conditional probability of recapturing an adult bird at least once in a particular year, given that it did survive and return to the area where it was present in the previous year. On the other hand, Klicka (1994) estimated survival rate based on only two years of data and defines this rate as individuals surviving from one breeding season to the next (excluding net mortalities). He experienced a survival rate of 55% (n = 29 surviving) for all adult *G. t. insperata*, 59% (n = 22 surviving) for AHY males, and 43% (n = 7 surviving) for AHY females. When considering just territory holding males, 81% (n = 16) returned the next breeding season (Klicka 1994).

While survival rates cannot be accurately measured with two years of data, this study shows estimates of survival rate which were lower than those found by Klicka and MAPS. Of the 71 individuals banded in 2008, close to 34% (n = 26) were recaptured in 2009. Of those recaptured, 69% (n = 18) were netted in the same territory both years. The remaining 31% (n = 8) were netted in different territories (average distance of 0.168 ± 0.061 km from the original territory) in 2008 and 2009. This lack of movement between field seasons supports the sedentary behavior of Brownsville Yellowthroats seen by Klicka (1994) in the LRGV. The severe habitat fragmentation may not be the cause of low survivorship values estimated here because the habitat was contracted when Klicka (1994) conducted research two decades earlier. Some other contributing factor(s) must exist, such as the elimination or loss of habitat that was previously fragmented.

Linear Density

If the shoreline of the River acts as a highway for gene flow, the density of individuals should be weighted more heavily in favor of sites near the River. This did not appear to be the case. When considering the density of individuals banded and all those individuals encountered (i.e. individuals banded + individuals seen or heard who were not banded) in 2008 and 2009, there is no significant statistical difference between sites near to and far from the River. Therefore, individuals appear to be distributed evenly among this area in no discernable pattern. Factors previously thought to be favorable, such as suitable habitat along the River and around resacas near the River, do not appear to be limiting factors for Brownsville Yellowthroats in the LRGV.

Population Structure

Since suitable riparian habitat for *G. t. insperata* becomes more dispersed south to north, individuals on or near the Rio Grande River should be more closely related than northern individuals. However, STRUCTURE results, estimations of expected heterozygosity (as an index of variation), and relatedness values all point to the existence of one admixed population with low genetic variation. STRUCTURE indicated, with and without prior knowledge of capture locality, that the presence of one population is the most likely situation occurring in this study system. Current literature indicates that when STRUCTURE cannot identify population structure based on genotypic frequencies, prior knowledge of capture locality can be used as supplemental

information to further assess population subdivision (Corander et al. 2003; Corander and Marttinen 2006; Hubisz et al. 2009). However, with the addition of collection localities, no population subdivision was detected. All other software analyses support STRUCTURE's prediction of a single population. This is seen in the observed and expected heterozygosity values (0.65 and 0.66, respectively), estimated using CERVUS, where this single population appears to be in or near Hardy- Weinberg Equilibrium with random mating occurring. RELATEDNESS estimated a value of 0.0553 for the entire population indicating low levels of relatedness (i.e. distant cousins). RELATEDNESS values support that gene flow is occurring and does not support any population structure. This low level of relatedness could support what was suggested by Klicka (1994), that the subspecies is not philopatric. Relatives do not appear to defend territories near each other. This indicates that offspring are dispersing and are not returning to defend territories in the vicinity of their birth place. Further analysis should be done to determine if this is male or female biased dispersal.

Genetic Markers

The quantity and quality of genetic markers used plays a role in population genetic studies (Queller et al. 1993). Too few markers can affect estimates of population structure, amount of gene flow, and many other genetic factors. The addition of different microsatellite loci and/or alternate genetic markers should lend greater confidence in the existing estimates of population structure. For example, in this study, no sample records came from Willacy or Starr counties because Brownsville Yellowthroats are not known to exist or breed

in these two counties of the LRGV. There are future plans to conduct presence/absence research of breeding pairs in southern Willacy and eastern Starr counties (Conway, pers comm.). If breeding Brownsville Yellowthroat pairs are discovered there, expansion of sampling localities to these additional south Texas counties might show subpopulations that are more distinct.

Population Model

Based on the distribution of wetlands and expected patterns of gene flow, the source-sink metapopulation model should be the model best fit to describe this subspecies. Although the Lower Rio Grande River Valley suffered significant habitat fragmentation and loss, the Brownsville Yellowthroat population appears to be completely panmictic, with little genetic structuring occurring throughout at least the two southernmost counties of Texas (Cameron and Hidalgo). All of the population models described earlier, less one (closed model), could potentially be used to describe the Brownsville Yellowthroat. However, given these data from this study, the population fits the open model. The population is characterized by panmixia and it cannot be subdivided into local subpopulations, thereby, eliminating the closed and metapopulation as sufficient models to describe this system.

Although the current system fits an open population model, there is potential that the system could fit the open or the metapopulation model if additional research shows the Brownsville Yellowthroat to be actively breeding in Tamaulipas, Mexico. The open population model would still be applicable if a

large number of unpublished Brownsville Yellowthroats are residing in Mexico and randomly mating with those found in the US. But, either of the metapopulation models could also be valid if there is any subpopulation structure found between Mexico and the U.S.. The source-sink model would be used if the population in the U.S. was acting as a source and supplying individuals south or if the population was acting as a sink where individuals were being removed from the subpopulation at a higher rate than being added. A patchy metapopulation model would be the best fit if those Brownsville Yellowthroats found in the U.S. are a mere subset of the entire population or belong to a much larger patch extending into Mexico. If Brownsville Yellowthroats are found breeding in Tamaulipas, a new dynamic could alter those conclusions drawn from in this study.

Subspecies

At Santa Ana NWR (western sampling site; Figure 7), concerns were raised that individuals sampled here potentially belonged to the western Rio Grande Common Yellowthroat subspecies, *G. t. chryseola* (Wolfe 1956), despite an estimated 100 km between *G. t. insperata* and *G. t. chryseola* ranges (Klicka 1994; Figure 5). However, morphological characteristics such as wing chord and primary feather measurements, which can serve as a useful guide in discriminating between *G. trichas* subspecies, supported that most individuals belong to *G. t. insperata*. *G. t. chryseola* are slightly larger in overall size than *G. t. insperata. G. t. chryseola* is characterized by wing length ranges from 51 to 61 mm (51 to 58 mm for females and 53 to 61 mm for males), tail length ranges

from 48 to 57 mm (48 to 55 mm for females and 50 to 57 mm for males), and the difference between the 9th and 4th primary feather (p9-p4) ranges from 0 to 4 mm (Pyle 1997). In contrast, *G. t. insperata* wing length ranges from 50 to 57 mm (50 to 55 mm for females and 52 to 57 mm for males), tail length ranges from 46 to 53 mm (46 to 52 mm for females and 48 to 53 mm for males), and p9-p4 ranges from -4 to 1 mm (Pyle 1997; Table 10).

Individual band number 15077045 was potentially a member of the west Texas subspecies. All morphological measurements from this individual fell within the ranges that Pyle described for *G. t. chryseola*; both wing length and exposed culmen length exceeded the range of *G. t. insperata* and were consistent solely with that of *G. t. chryseola*. This individual presumably defended a territory at Santa Ana during the year it was banded. Every race has extreme individuals who exhibit characteristics typical of the average condition of traits in a neighboring race (Behle 1950). Because of this finding, further genetic analysis should be conducted. The microsatellite markers used in this study may not distinguish *G. t. insperata* from *G. t.* chryseola, genetically. More genetic markers should be used in conjunction with the current loci in an effort to tease apart possible *G. t. chryseola* individuals from the Santa Ana NWR data set. It would be especially useful if a set of genetic markers be developed that reliably distinguished *G. t. insperata* from *G. t. chryseola*. In addition, samples are needed from many confirmed west Texas *G. t. chryseola* individuals in order to build a catalog for the sake of comparing unknown individuals.

TABLE 10. *Geothlypis trichas insperata* and *G. t. chryseola* can be differentiated by a standard set of morphological characteristics. Ranges of these characteristics according to Pyle (1997) are provided along with measurements and means for individuals banded at Santa Ana NWR.

	Pyle *G. t. insperata*	Band 2520 8445 6	Band 1530 7703 5	Band 2050 1139 0	Band 1530 7704 1	Band 1530 7704 2	Band 1530 7704 3	Band 1530 7704 4	Band 1530 7704 5	Band 1530 7704 6	Band 1530 7704 7	Roy Santa Ana (mean ± se)	Pyle *G. t. chryseola*
wing length (mm)	50-57	56	55	53	55	54	54	53	59	52	54	54.5 ± 0.62	51-61
tail length (mm)	46-53	53	51	x	49	51	51	53	51	44	49	50.2 ± 0.91	48-57
p9-p4 (mm)	-4 to 1	-0.9	0	x	-0.9	-1.5	-2.3	-1.7	0	0	-1.1	0.93 ± 0.27	0 to 4
exp culmen (mm)	10.7-12.2	11.8	11.7	x	12	12.3	12	12.3	12.8	12.3	12.2	12.16 ± 0.11	10.5-12.4

Population Status

The breeding status of the Brownsville subspecies in Tamaulipas, Mexico is currently unknown, with no confirmed breeding records in at least a decade (Klicka 1994). Previously, in August of 1908, F.B. Armstrong documented an extant population of the Common Yellowthroat in Matamoros, Tamaulipas, Mexico (Phillips 1911). At the time, those birds were considered a part of the Northern Yellowthroat subspecies (*G. t. brachidactyla*). In 1988, Klicka (1994) could find no support, besides Armstrong, in the literature for the existence of any Common Yellowthroat breeding populations in Tamaulipas, Mexico. During his study, Klicka documented a population of breeding Common Yellowthroats in Tamaulipas, but that group could not be confidently associated with the Brownsville subspecies. He noted that gene flow between the groups is likely inhibited by an expanse of unsuitable habitat though which no Yellowthroats are known to cross.

Even though it is a questionable breeder in Mexico, the Brownsville Yellowthroat is known to occur along the Mexico side of the Rio Grande River, as movement into Mexico on the immediate opposite side of the River was witnessed (personal observation). Due to these observations, it is inferred that the birds are using some resources (e.g. food or habitat) south of the U.S. boarder, but the extent of use is speculation at this point. It is logical to think these birds utilize similar habitat in Mexico because the structure of the Mexico bank and vegetation along the River are nearly identical to the U.S. bank. I

suggest that additional research should be conducted in wetland areas south of the U.S./Mexico border to ascertain the breeding status, distribution, and population density of the Brownsville Yellowthroat in Tamaulipas, Mexico.

The Brownsville Yellowthroats found in Texas have not been studied as extensively as many other warblers found in this state and the surrounding region, but substantially less research has been conducted on Brownsville Yellowthroats in Mexico. So, as isolated as this subspecies is in the United States, this subspecies' population could be larger than previously thought with a vast proportion possibly extant south into Mexico. The northern limit to the Brownsville Yellowthroat's range is relatively understood, however, the southern limit of this subspecies is almost completely unknown. Therefore, all approximations of population size for the Brownsville Yellowthroat could be gross underestimates.

Conservation Concerns

From an ecological standpoint, the range of the Brownsville Yellowthroat in Texas has been severely contracted and it is listed as a "Species of Concern" by the U.S. Fish and Wildlife Endangered Species Program. The San Francisco or Salt Marsh Yellowthroat (*G. t. sinuosa*) is another subspecies of the Common Yellowthroat whose life history is comparable to that of the Brownsville Yellowthroat. The Salt Marsh Yellowthroat is a state and federal species of concern as described by the California Department of Fish and Game and the

U.S. Fish and Wildlife Service. It is a year-round resident primarily found around the San Francisco bay area and it, like the Brownsville Yellowthroat, has experienced persistent habitat destruction (SFBNWR 1974). The Salt Marsh Yellowthroat population has declined 80-95% in the last decade (Foster 1977). Based on data collected by many past studies, Gardali and Evens (2008) estimated the current population size to be between 1000 to 2000 individuals. Therefore, Foster (1977) has recommended the Salt Marsh Yellowthroat as a candidate for Endangered Species status in California.

As the other of only two sedentary Yellowthroat populations, the Brownsville Yellowthroat has not been studied as extensively as the Salt Marsh Yellowthroat and has not benefited from the same ecological attention and conservation efforts as its California counterpart. With a considerably smaller estimated population size (nearly 1/10 the size of the Salt Marsh Yellowthroat) and a species of arguably more concern, the Brownsville Yellowthroat is considered neither Threatened nor Endangered.

The Brownsville Yellowthroat is more than a species of concern that needs to be recognized at an international level. Plans to conserve its habitat and the extant populations need to be put into place and adhered to by all organizations in the LRGV. Restoration of habitat and, at the very least, prevention of further habitat destruction is essential. Klicka (1994) lays out several management practices that the Brownsville Yellowthroat would greatly benefit from; in particular, synchronized/scheduled mowing and grazing periods

along the River and around resacas that do not conflict with the breeding season would afford the breeding pairs enough time to rear offspring and give the population a chance to grow in the United States. The survival of the Brownsville Yellowthroat is potentially at a critical point where human decisions can mean the difference between population growth and the extinction of this rare subspecies. Most important to this pursuit is the need for up-to-date information regarding the presence and viability of *G. t. insperata* in Mexico.

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