# Section 6 (Texas Traditional) Report Review

Form emailed to FWS S6 coordinator (mm/dd/yyyy): 11/4/2010				
TPWD signature date on report: Yes				
Project Title: <u>Havs County Karst Invertebrate D</u>	fistribution And Cave Development			
Final or Interim Report? Final				
Grant #: E-105				
Reviewer Station: Austin ESFO				
Lead station concurs with the following comm	ents: NA (reviewer from lead station)			
Interim Report (check one):	Final Report (check one):			
Acceptable (no comments)	Acceptable (no comments)			
Needs revision prior to final report (see comments below)	Needs revision (see comments below)			
Incomplete (see comments below)	Incomplete (see comments below)			

## Comments:

Please spell out acroymns the first time they are used and then use the acronym in the rest of the document. For example, karst fauna regions is first used in the second paragraph of the introduction; however, the acronym is not provided until the third paragraph. Also, NDM is first used in the fourth paragraph of the introduction (p.2); however, it is not spelled out until the sixth paragraph on p.6.

Please correct grammatical errors throughout the document including comma errors and several spacing errors after periods. Also, the first sentence in the fourth paragraph on p. 6 is missing a period.

It is not clear if one cave contains three Texella spp. in figure 5.

Please label the KFRs in the actual figure (figure 9) because it is difficult to discern which KFR is which from a black and white copy.

The word "artifactual" is misspelled on p. 40.

Please insert page numbers.

The word Cicurina should be italicized in the last paragraph on p. 11.

FINAL REPORT

# As Required by

# THE ENDANGERED SPECIES PROGRAM

# TEXAS

Grant No. TX E-105-R

Endangered and Threatened Species Conservation

# Hays County karst invertebrate distribution and cave development

Prepared by:

Kathleen O'Connor



Carter Smith Executive Director

Clayton Wolf Division Director, Wildlife

12 August 2010

# FINAL REPORT

<b>STATE:</b> <u>Texas</u>	GRANT NUMBER:	<u>TX E-105-R</u>
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**GRANT TITLE:** Hays County karst invertebrate distribution and cave development

**REPORTING PERIOD:** <u>1 Oct 08 to 31 Aug 10</u>

# **OBJECTIVE(S):**

To determine the distribution of karst invertebrates in Hays County by sampling caves, and using hydrogeologic evaluations of those caves to establish management units for the species.

# Segment Objectives:

Task 1. Sept – Dec 2008. Arrange site access for 20 caves in Hays County, with a preference for sampling broadly across karst terranes and in previously unsampled caves.

Task 2. Jan 2009 – Apr 2009. Field work to sample 20 caves and karst features.

Task 3. May 2009 – Sept 2009. Curate and identify collected specimens, write up the hydrogeologic evaluations, test the endemicity analysis methods, delineate management areas for karst fauna in Hays County.

# **Significant Deviation:**

None.

# **Summary Of Progress:**

Please see Attachment A (pdf).

Location: Travis County, Texas.

**Cost:** Costs were not available at time of this report, they will be available upon completion of the Final Report and conclusion of the project.

Prepared by: <u>Craig Farquhar</u>

**Date:** <u>12 Aug 2010</u>

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Approved by:	C. Craig Farquhar	Date:	<u>12 Aug 2010</u>

2010



# Hays County Karst Invertebrate Distribution and Cave Development



Cave entrance in Hays County

Prepared for County of Hays, Texas

15-July-2010

# Abstract

The objective of this study is to explore a variety of methods for designating management units (or subdivisions of ranges used for recovery planning purposes) for cave species in Hays County, Texas. The distribution of 45 rare karst species was determined throughout Hays County by sampling caves and compiling historical locality data. We performed analyses of endemicity using three methods, Parsimony Analysis of Endemicity, NDM, and a simple numerical graph. These results demonstrated a high degree of endemicity located around San Marcos Springs.

Hydrogeologic evaluations of cave and spring localities within the geological context aided mapping habitat continuity across the county. Multiple iterative maps were prepared based on published karst terrane datasets to evaluate alternative areas for karst species management units. Multiple techniques for evaluation of biological spatial data within these areas are proposed, and the pros and cons of each are discussed. The maps produced herein are a practical starting point for land managers needing to make decisions about continuity of karst habitats and similarity of species composition across the county.

## Introduction

Hays County lies within the Edwards Plateau ecoregion of central Texas, an area characterized by karst topography and underground drainage that supports many endemic and unique aquatic and terrestrial faunal assemblages (Bowles and Arsuffi 1993). Compared to surface species, cave-adapted fauna generally have small geographic ranges and high levels of endemism, making them biogeographically distinct (Culver and Holsinger 1992, Christman et al. 2005). Sixteen terrestrial karst invertebrates in this ecoregion are federally listed as threatened or endangered species, with several known from only one locality (Campbell 2003, USFWS 2004). Six aquatic species (known from springs and caves) are federally listed as threatened or endangered species, two of these are only known from one locality (Chippendale et al. 1998, USFWS 2007). One site, an artesian spring in Hays County, has eleven endemic species documented, representing 40 percent of all species sampled there (Culver and Sket 2000).

The purpose of identifying areas of endemism (and subsequent management units) for rare and endangered karst species in central Texas is to delineate recovery regions (USFWS 1994 and 2008). Recovery regions dictate the geographic spread of numbers of individuals or populations needed to delist or downlist a species. They are also used in determinations of jeopardy that impact the outcome of Endangered Species Act permitting. In many cases the purchase of conservation land is also dictated by recovery regions, with the goal of preserving populations of species across their known range. An area of endemism is almost always one of high conservation priority due to the presence of many narrowly ranged species that are typically restricted to such areas (Stattersfield et al. 1998, Margules and Sarkar 2007).

The U.S. Fish and Wildlife Service (USFWS) established management units, also called karst fauna regions, for the federally-listed karst invertebrates in Travis, Williamson and Bexar counties (USFWS 1994 and 2008). These karst faunal regions were created using a mix of data on habitat continuity, karst fauna endemism, and species ranges (Veni 1992, 1994, and 2002). Habitat continuity was evaluated by examining geologic controls on cave development, and included detailed analyses of specific cave morphology in relation to probable vicariant mechanisms for cave adapted species. Vicariant mechanisms include faulting and river downcutting, which isolate blocks of rock formations that contain caves. Degrees of endemism and species ranges were mapped onto those habitat blocks *post hoc*.

This approach provides a way of estimating the potential for communication among modern species populations while also identifying limits to faunal assemblages across a region.

Various authors have also used genetic data to show patterns of population connectedness in cave adapted species in central Texas. Paquin and Hedin (2004) examine morphologic and genetic (mtDNA) data of *Cicurina* spiders, and show relative changes in populations between designated karst fauna regions (KFRs). White (2006) uses gene data in this group to support hypotheses regarding hydrogeologic history of the region, and suggests that KFRs established by USFWS do not reflect the biogeographic history of this taxon. Krejca (2005) tests *a priori* hydrogeologic hypotheses against gene trees (mtDNA) for two genera of aquifer adapted isopods, and finds that patterns of relatedness follow the different origin (freshwater vs. marine) of each taxon. Lucas (2008) gathered both mtDNA and nuclear DNA in *Eurycea* salamanders and performed analyses that indicated complete isolation of the populations, therefore recommended that each population be considered a distinct management unit. Each of these studies supports gene trees and relationship networks that can be mapped to create management units.

In this paper, similar methods approved by USFWS are used for drawing karst fauna regions (Veni 1992, 1994 and 2002). We also examine different methods for performing endemicity analyses, including PAE - Parsimony Analysis of Endemicity and NDM (Rose 1988, Szumik and Goloboff 2004), and discuss the results of each method in regards to efficacy in endangered species management.

## Background

#### Hays County Geology

The geology of Hays County is spatially variable, ranging from younger clastic rocks in the southeastern portion of the county to progressively older carbonate rocks towards the northwest. The ages of these rocks exposed on the surface from youngest to oldest are: Quaternary alluvial deposits found in river and creek valley bottoms (Leona Gravel Fm., Onion Creek Marl, and various alluvial members); Late Cretaceous clay/shale (Navarro Group); Late Cretaceous chalk, limestone and marl (Pecan Gap Chalk, Austin Chalk); Mid Cretaceous limestone and marl (Eagle Ford Formation, Buda Limestone, Del Rio Clay); Early Cretaceous limestone of the Edwards Group (Georgetown Limestone, Person Formation, Kainer Formation, Fort Terrett Limestone); Early Cretaceous limestone and sandstone of the Trinity Group (Upper Glen Rose Limestone, Lower Glen Rose Limestone, Cow Creek Limestone, Hensell Sand). The geologic map for Hays County shows the spatial distribution of rock types and formations in the county (Figure 1). Detailed mapping of Edwards Group formations and members was performed by Hanson and Small (1995), and mapped units from other lithologies come from the Geologic Atlas of Texas (TNRIS 2010) These units from different ages have been juxtaposed to each other by Miocene faulting of the Balcones Fault Zone.



Figure 1. Geologic map of Hays County.



**Figure 2**. Stratigraphic column for Hays County geologic units showing hydrogeologic units relative to the Edwards Aquifer.

#### Regional Geologic History

The pre-Cretaceous geologic history includes deposition of about 5,000 feet of Paleozoic carbonates, sandstone, and shale during the Early Cambrian (Flawn 1956). These sedimentary rocks were intensely uplifted, faulted and folded during the Ouachita orogeny peaking in the Late Pennsylvanian through Early Permian. A wide, shallow sea formed in a basin within the region and was eventually uplifted and aerially exposed by the end of the Paleozoic Era. During the Triassic and Jurassic Periods, most of central and west Texas was exposed to erosion as the Llano uplift created a topographic high in central Texas. The surrounding basin filled with Triassic red beds of the Dockum Group. By the end of the Jurassic, a large sea prograded westward and eventually covered most of central and much of west Texas.

The primary karstic geologic units in the area are Cretaceous age limestone, and include Lower Cretaceous (Glen Rose Limestone, Edwards Group) and Upper Cretaceous (Del Rio Clay, Buda Limestone, Eagle Ford Group, Austin Chalk) and are shown in Figures 1 and 2. These carbonate rocks were deposited in a series of cycles where shallow oceans covered the region then regressed seaward (southeast) and prograded back to submerge the area. Thick sequences of limestone formed as a result of this process, and provide the primary framework for present day aquifers.

In the early Cenozoic time, these rocks were heavily faulted as the ancestral Gulf of Mexico to the southeast subsided. This high angle normal faulting produced as much as 365 meters of vertical displacement in the area now referred to as the Balcones Fault Zone (BFZ). The BFZ is defined by Cretaceous carbonates dissected by this network of faults and related fractures, including series of ramp-like structural features interconnected with major faults that strike generally east-northeast. Bedding on the downthrown fault blocks exhibits a steeper southeastward dip relative to the upthrown fault blocks of the Hill Country region (Maclay and Small 1986).

The BFZ is the principal structural geologic feature in the Plan Area, and has a great influence on groundwater flow. Fracture planes can act as conduits for or barriers to groundwater movement, depending on the amount of offset, stratigraphic juxtaposition, and post-tectonic erosional and dissolutional processes. The contact between the Hill Country and the Balcones Fault Zone was determined structurally from the up-dip edge of major faults juxtaposing older Trinity Group rocks against younger Edwards Group rocks (Barker et al. 1994). Development of secondary porosity along fault planes heavily influenced the diagenetic processes occurring throughout the Cenozoic and into the Quaternary, including extensive karstification.

In areas of streams and rivers there has been some deposition of alluvial deposits, mostly silt, sand, and gravel that thinly cover the eroded limestone surface. A more detailed explanation of the regional geologic history can be found in Rose (1972), Maclay and Small (1986), and Barker et al. (1994), as well as many others.

## Karstification

Karst occurs in soluble rock, primarily limestone, which covers all but the southeastern portion of Hays County. Not all limestone is heavily karstified in the county. In 2008, Zara Environmental LLC looked at the distribution of known karst features relative to bedrock geology in order to designate five types of bedrock outcrop where karst features are likely to form. These outcrops are referred to as karst terranes and are, from youngest to oldest, the Buda limestone, the main outcrop of the Edwards Aquifer (Georgetown, Person and Kainer formations), outliers of the Edwards Group (Fort Terrett Limestone) that are geographically isolated from other outcrops of Edwards Group limestone, the lower member of the Glen Rose Formation, and the Cow Creek Limestone. During this study we targeted these karst terranes for biological surveys and compared collection data to hydrogeological features present throughout. These efforts resulted in the delineation of five Hays County KFRs.

## Karst Fauna Regions

Following analysis of the topographic, geologic, hydrologic and biologic data reviewed for Hays County, we delineated five KFRs. The karst terranes published in the Hays County Habitat Conservation Plan (HCP) (Zara Environmental 2008) provided the geologic framework to compare to independent analyses of karst species distribution.

#### Species Distributions

The list of 45 Hays County rare species used for this study was compiled using a variety of sources, including the database of karst invertebrates in the Texas Memorial Museum (maintained by James Reddell) as the foundation for species range data. Additionally, we conducted interviews and obtained reports as described in the earlier document by Zara (2008). We omitted cave species known to occur widely throughout the region, for example *Cambala speobia* millipedes and *Brackenridgia cavernarum* isopods. While these species are important for the cave community, their lack of differentiation at the scale of a single county makes them less useful for creating management units at this local level.

## Parsimony Analysis of Endemism (PAE) and NDM Analyses

Parsimony analysis is widely used in phylogenetic studies, but can also be used to delimit areas of endemism within a region (Morrone et. al 1999, Garcia-Barros 2002 et al., Sigrist and Barros de Carvalho 2008) The parsimony analysis of endemicity (PAE), originally proposed by Rosen (1988), is a biogeographical tool that aims to classify areas by the most parsimonious solution based on the shared presence of taxa. Morrone implemented a tractable user-friendly algorithm into publicly available software (1994). His method subdivides a region into a square grid and uses a cladistic analysis to categorize the grid cells into a cluster based on their shared taxa. The most parsimonious solution contains clusters of cells that are designated as areas of endemism.

PAE does not take into account spatial relationships between cells. When a cluster in the most parsimonious solution contains grid cells that are not congruent with each other, a single area of endemism is split into more than one geographic area. Such a result usually does not permit any plausible biogeographic explanation of the observed endemism. This situation also presents problems for conservation planning because non-adjacent cells do not form a spatially coherent network of conservation management areas.

To address these issues, Szumik *et al.* (2002) proposed a different method, based on spatial relations, to determine areas of endemism. This method, called NDM (from "eNDeMicity"), was updated in 2004 (Szumik and Goloboff 2004). NDM constructs an objective function that is a measure of endemism (see Section 2) and then tries to find the optimal spatial solution that maximizes the value of this objective function. It differs from a PAE in three important ways (Szumik *et al.* 2002):

i. For areas of endemism, higher scores are given for contiguous areas rather than discontinuous ones.

- ii. A continuous range of scores, as opposed to 0 for non-endemic and 1 for endemic, is used by NDM to quantify a degree of endemicity for a species. For instance, a species with fewer records from outside the area is more endemic than a species with more records outside. This is a useful feature in many conservation prioritization contexts.
- iii. Different areas of endemism, as determined by NDM, may overlap. However, since each will have a quantitative endemicity score, produced by its unique complement of species, these different overlapping areas may have different conservation value.

# Methods

The methods section is organized according to project components, and also by a timeline. Our first step included gathering species data, both in the field and by literature review, and this was followed by analyses. The endemicity analyses (PAE and NDM) were performed by the Sarkar laboratory at The University of Texas at Austin using the biogeographic dataset. Zara Environmental geologists and biologists used the same dataset independently to mimic existing methods for KFR delineation.

Zara Environmental conducted biological surveys in caves across karst terranes in Hays County, Texas to assess distribution of 45 rare karst fauna across geologic and hydrologic barriers. Collected data were compiled with historical records of rare fauna across the county and evaluated for the purpose of identifying areas of endemism, and for establishing management units within the county for species conservation.

#### **Biological Surveys**

Biological surveys of Hays County caves were conducted from February 2009 to March 2010. At each cave surveyed, positional data were recorded using a hand held Magellan Explorist Global Positioning System (GPS) receiver and estimated position errors (EPE) were recorded. All features surveyed were also photographed.

Biological surveys in each cave were conducted with a minimum of two persons. Visual searches for organisms were performed by thoroughly inspecting all surfaces, including the walls, floor, and examining the insides of any cracks and crevices using a headlamp. The undersides of loose rocks were inspected with the naked eye, occasionally aided by the use of a jeweler's loupe for magnification. The floor substrate, including substrate underneath rocks, was also thoroughly examined. Collected organisms were placed in plastic bottles containing 95% ethyl alcohol for later identification. Collected specimens were taken back to the Zara Environmental lab for examination and taxonomic evaluation. All collections were assigned a collection number, placed in glass vials with permanent labels, and entered into a Microsoft Access database. All collected specimens were delivered to Dr. James Reddell of the Texas Memorial Museum (TMM) for curation.

Table 1. Features surveyed in Hays County,	Texas from	February	2009 to
March 2010.			

Feature Name	Feature Type	# of Visits
6F Cave	Cave	1
Antioch Cave	Cave	1
Beyond the Pail Cave	Cave	2
Big Mouth Cave	Cave	1
Blanco Robusta Swallet	Feature	4
Cantera Ranch Cave	Cave	1
Cliff Cave	Cave	1
Corrie Smith Cave No. 1	Cave	1
County Line Bat Cave	Cave	1
Dahlstrom Cave	Cave	1
Feature 42 V	Feature	1
Feature 51	Feature	1
Flocke's Cave	Cave	1
Freeman Crawl Cave	Cave	1
Fritz's Cave	Cave	1
Grapevine Cave	Cave	1
Hackberry Cave	Cave	2
Harwell's Greenhouse Pit	Cave	1
Harwell's Stinkpot Cave	Cave	1
Hays Ranch Bat Cave	Cave	2
Hobbit Hole	Cave	2
Hole in the Ground	Cave	1
Hoskins Hole	Cave	1
Jeanette's Cave	Cave	1
Kira's Sink	Sink	1
Kiwi Sink	Sink	3
Kunkel Cave	Cave	1
Lona's Sink	Feature	1
Lost Springs Cave	Cave	1
McCarty Cave	Cave	2
Mouse Hole Cave	Cave	2
Porcupine Cave	Cave	1
Possum Haw Cave	Cave	1
Pucker Cave	Cave	2
Pulpit Cave	Cave	2
Root Beard Cave	Cave	1
Sink #2	Sink	1
Sky Ranch Cave	Cave	1
Taylor Bat Cave	Cave	1
Twin Chimney Cave	Cave	1
Unknown Name	Sink	1
(Rattlesnake Sink)		
Wimberley Bat Cave	Cave	2

Great effort was made to gain access to those sites located on private land. The Texas Speleological Survey (TSS) database was accessed in order to target previously unsurveyed features of interest. This information was used in conjunction with Hays County tax maps in order to obtain property ownership information. All caves surveyed from February 2009 to March 2010 are listed in Table 1.

#### Designation of Karst Fauna Regions

Methods applied in this study are similar to those previously approved by USFWS in other counties to create KFRs for Hays County. This is an iterative methodology resulting from analyzing topographic, hydrologic, geologic, and biologic information. Defining specific regions is a spatial analytical process based on pre-existing data and data generated from the scope of this investigation. The starting point for delineating KFRs for Hays County is the Karst Terrane Map prepared for the Hays County HCP by Zara Environmental (2008). This map defined five distinct geologic units that contain significant caves and karst features, classified as 1.) Cow Creek; 2.) Edwards Outliers; 3.) Lower Glen Rose; 4.) Georgetown/Edwards; and 5.) Buda Limestone (Figure 3). This geo-spatial dataset generated by Zara (2008) was imported into a geodatabase using ArcGIS 9.3 software to allow for expanded analysis within a Geographical Information System (GIS) framework.

The karst polygons defined in the Hays County HCP provide an initial filter to subtract areas without known karst development from analysis. Known localities of caves or karst features containing karst biota (terrestrial and aquatic) are then plotted on these polygons. These features are defined as locality sites. There are several karst terrane polygons that do not contain a locality site, for example the karst units at the northern tip of the county, many patches of Buda Limestone at the northeast margin of the Georgetown/Edwards, the small, isolated Edwards caprocks in the north central part of the county, and the isolated Georgetown/Edwards plateaus in the center of the county (Figure 3). Since there are no biologic data associated with these polygons, we proceeded with the assumption that they would have a faunal assemblage related to geographically proximal units.

The remaining polygons with locality sites are then compared to maps of species ranges and indices of diversity (using percent of shared species and other endemism indices, PAE and NDM). Patterns of karst species endemicity are identified to determine if an additional geographic area should be separated from any existing contiguous polygon. If any pattern is recognized, then possible geologic, geographic, or hydrologic boundaries are considered that could serve as significant barrier to troglobite migration. These possibilities include rivers that incise karstified limestone to sufficiently separate contiguous habitats, faults that offset karstified strata, and groundwater levels that may isolate suitable habitats for both aquatic and/or terrestrial troglobitic species. This step results in numerous karst area polygons that all have records of karst species, but the geometry of polygons is solely defined by previously mapped geologic units, prior to further analysis of species distribution.



Figure 3. Karst Terranes map from Hays County HCP shows karst geologic areas in the study area.

# Endemism Index (percent of shared species method)

The Endemism Index was calculated for each of the delineated Hays County KFRs by subtracting the average percent shared troglobites in each area from the percent of endemic species (Veni 1992, 1994). As per Veni, the endemism indices were calculated after the KFRs were delineated. Degrees of endemism are classified as follows (Veni 1994):

- 100 to -61: High non-endemism. Areas with no restrictions to migration; biologically homogeneous with other areas.
- 60 to -31: Moderate non-endemism. Areas with minor restrictions to migrations which cause no apparent reductions in biologic homogeneity with other areas.
- 30 to 0: Low non-endemism. Areas with restrictions to migration in which there are some minor differences in species distribution while there is overall biologic homogeneity with other areas; also areas where there has been insufficient time to speciated since the development of restrictions.
- O to 30. Low Endemism. Areas with significant restrictions or minor barriers to migration; biologically distinct from, yet similar to other areas; also areas with major barriers to migrations where speciation has recently begun to affect local fauna.
- 31 to 60: Moderate endemism. Areas significantly bounded by barriers to migration, but where limited migration may still be possible; biologically distinct but with several species in common with other areas.
- 61 to 100: High Endemism. Areas bounded by barriers to troglobites migrations; biologically distinct from other areas with few, if any, common species; species have troglobitically advanced since the development of migration barriers.

## Parsimony Analysis of Endemism (PAE) and NDM Analyses

Occurrence data for the species were restricted to the karst regions of Hays County. In all, there were 128 occurrence records corresponding to 45 species; 46 species including *Cicurina bandida* (Appendix A). The study area, covering almost all of Hays County except for the northern tip which was not represented in the data set, was modeled as a 5 km  $\times$  5 km grid. There were 90 cells, each of which was assigned a unique number (Figure 4). Twenty-seven cells contained occurrence records. The 5 *km* resolution was selected because a preliminary analysis using NDM and "all species" (see below) gave higher endemicity scores for units at this resolution compared to a 2.5 *km* and 10 *km* resolution.

Terrestrial and aquatic species were analyzed together as well as separately. Because of taxonomic uncertainties within the spider genus *Cicurina* (Pierre Paquin pers. comm.), two types of analyses were performed: (i) in one set of analyses, the genus Cicurina was considered to be comprised of three species, *Cicurina ezelli, C. russelli* and *C. ubicki*; (ii) in the other set of analyses, with a "modified" data set, *C. bandida* was considered as a single species which embraced *C. ezelli, C. russelli* and *C. ubicki*—these analyses included new cells which had *C. bandida* records. This distinction only affected the analyses of all species and that of terrestrial species (because *Cicurina* is a terrestrial spider). Thus, there were five sets of analyses: *all species, modified species, terrestrial, modified terrestrial,* and *aquatic.* 



**Figure 4.** Study Area with All Occurrence Points and Operational Geographical Units (Cells). Occurrence points (black dots) for data collected from the karst regions (in orange) of Hays County, Texas. In several instances, a single black dot represents occurrence points of several species at one location. The co-ordinate system is UTM 14 North.

The PAE was performed with the software package, TnT (Version 1.1; Goloboff *et al.* 2003). Typically optimal (exact) solutions can be found using TnT in a reasonable amount of time for data sets with 15 -30 cells (Goloboff *et al.* 2008). For larger data sets, the use of a heuristic search algorithm becomes necessary to solve problems in reasonable time even with high performance computers. These heuristic methods were used for this analysis. However, to assess the performance of these heuristic methods (which may produce sub-optimal results), optimal solutions were obtained for the smallest data set (*modified*).

*terrestrial*). The results were identical to the heuristic solutions. This provides some reason to expect that, in general, the heuristic solutions are not marred by problematic sub-optimality.

Because of the relatively large size of the data set, the heuristic search algorithm used branch swapping between random trees for all the data sets. The best (most parsimonious) trees, as determined internally by the TnT algorithm, were stored and subsequently used to generate a consensus tree. The consensus tree was generated by using both a strict and a majority rule. The strict consensus tree contains only those clusters found in all the best (most parsimonious) trees whereas the majority rule consensus tree (at a cutoff of 50) contains all the clusters found in at least half of such trees (Goloboff *et al.* 2008). Both consensus trees and a map of synapomorphies were recorded for all the data sets.

The NDM software package (NDM/VNDM, Version 2.5 [Goloboff 2004]) computes endemicity scores for various sets of cells with the following formula (Szumik and Goloboff 2004). The score, *E*, for an area, *A*, with a fixed number of cells, *n*, is given by:

$$E = \sum_{j=0}^{n} V_j$$

where  $V_j$  is the endemicity score of the individual species *j*, and is given by:

$$V_j = \frac{p + (iF_i) + (aF_a)}{S + \frac{o}{F_o} + \frac{d}{F_d} + \frac{n}{F_n}}$$

where *p* is the number of cells in *A* in which species *j* is present, *i* is the number of cells in which species *j* is not present but is inferred as present because it is present in all of the surrounding cells, *a* is the number of cells in *A* in which species *j* is assumed to be present (*a* = 0 in this analysis), *S* is the total number of cells in *A*, *o* is the number of cells adjacent to *A* in which species *j* has been recorded, *d* is the number of cells adjacent to *A* in which species *j* has been recorded, *d* is the number of cells adjacent to *A* in which species *j* has been recorded, *d* is the number of cells adjacent to *A* in which species *j* has been assumed (*d* = 0 in this analysis), *n* is the number of cells outside of *A* and non-adjacent to *A* in which species has been assumed (*n* = 0 in this analysis). *F*<sub>i</sub>, *F*<sub>a</sub>, *F*<sub>o</sub>, *F*<sub>d</sub>, and *F*<sub>n</sub> are weights (between 0 and 1) attached to these numbers. The influence of inferred and assumed presence is made more or less influential by giving a score between 0 and 1 to the weights. The following default values provided by the program were used in this analysis: *F*<sub>i</sub> = 0.5, *F*<sub>a</sub> = 0.75, *F*<sub>o</sub> = 0.5, *F*<sub>d</sub> = 2, and *F*<sub>n</sub> = 0.5 (Szumik and Goloboff 2004). However, the only factors that influence this analysis are *F*<sub>i</sub> and *F*<sub>o</sub>. All species with *V*<sub>j</sub> > 0 are regarded as endemic.

Two partially overlapping areas can be considered as separate areas of endemism if different species contribute to the endemicity score, that is, different species are endemic to the two overlapping areas according to the criteria of NDM. Because the number of species in this analysis is relatively small, a set of cells was deemed an area of endemism if at least 50 % of the species were unique.

# Results

#### **Biological Surveys**

Fifty-six visits to 42 features were conducted throughout Hays County (Table 1). A total of 43 collected individuals were candidates for rare fauna, with the majority of those collected belonging to the spider genus, *Cicurina*. We combined these data with historic localities to create the base dataset (Appendix A). Using this dataset, we created maps of a selection of representative species' ranges in Hays County (Figure 5-7).



Figure 5. Range map of four *Texella* species found in Hays County.



Figure 6. Range map of three genera of karst invertebrates in Hays County.



Figure 7. Range map of five species of *Eurycea* in Hays County.

#### Karst Fauna Regions

Review of the species range maps show that the most unique zone of endemism occurs primarily around the San Marcos Springs area, resulting from aquatic species not found elsewhere in the county (Figure 7). This area is unique in comparison to other areas of the county because there are so many endemics in a very small geographic area (Longley 1981, Culver and Sket 2000). In our analysis, 24 out of 45 species occur only in this small area. This area of endemism is not reflected by geologic discontinuities in the base karst terrane map (Figure 3), so we decided that this warranted additional splitting of the Edwards/Georgetown Karst Terrane. The San Marcos Springs area is located within this karst terrane which covers a broad swath of the central portion of the county from southwest to northeast (Figure 3). San Marcos Springs is in the southern portion of this segment, so we identified likely natural boundaries separating it from the rest of the Edwards/Georgetown. To the north, the Blanco River provides the break from Edwards/Georgetown limestone in northern Hays County. To the west, The Bat Cave Fault significantly offsets the younger Person Formation from the Kainer Formation, both within the Edwards Group Limestone. Although both formations are karstified and contain numerous caves with karst biota, this is considered to provide a possible natural extent for aquatic species that live in the deeper portions of the Edwards Aquifer and are observed in the San Marcos Springs area.

The remainder of the species distributions showed no striking patterns, or instances where multiple taxa show the same geographic boundaries. Terrestrial invertebrates in some cases are known from only a single site, and in other cases (for example *Texella grubbsi*, Figure 6) are known from both sides of a potential restriction or barriers to modern migration. Thus the remainder of decisions regarding the creation of KFRs relies on information from a much smaller number of species.

Based on the range of the aquatic species *Eurycea pterophila*, we determined that combining the Glen Rose Limestone in the western portion of the county is warranted.

Another zone of lower endemism shows a signal from the PAE in the western portion of the county in Glen Rose Limestone. This review resulted in an intermediate KFR delineation with seven separate regions (Figure 8). The geographic extent of these intermediate areas is a direct reflection of the geologic polygons defined in the Hays County HCP Karst Terrane map, but has been divided into individual contiguous units and split by PAE results.

Review of species distribution across some adjacent intermediate KFRs indicates that no variability existed, so in those cases they are merged together into one final KFR. For example, caves with species in both Glen Rose intermediate KFRs have similar aquatic species (for example *Eurycea pterophila*), so they are joined. The "non-karst" area that separates these karst terrane polygons in plan view is a ridge of younger (Upper Glen Rose) limestone. It overlays the Lower Glen Rose, thus is actually a cap on an otherwise contiguous lateral band (figure 7). The cap is narrow enough that it may allow for lateral migration of terrestrial karst species underneath it, and provides no barrier to aquatic species movement. Therefore, they are grouped into a single KFR. Analysis of species in the Central Edwards Islands intermediate KFR (Figure 8) reflects similarities in aquatic species (for example *Eurycea pterophila*) to those found in both the Glen Rose intermediate KFRs, so this area has been included into one final KFR called the Western Hays KFR. The result of final grouping based on patterns of karst species distribution across intermediate

KFRs defines five KFRs for Hays County: The North Edwards KFR, The Western Hays KFR, The Bat Cave Fault Block KFR, the San Marcos KFR and The Pedernales KFR (Figure 9). A geologic cross-section of Hays County showing major geographic, geologic, and hydrologic features related to KFR delineation is shown in Figure 10. Distribution of rare fauna across the five Hays County karst fauna regions is shown in Figure 9.

# The North Edwards KFR

The North Edwards KFR includes primarily areas of Edwards Group limestone (Georgetown Limestone, Person Formation, Kainer Formation) northeast of the Blanco River. Two caves with karst species of concern are located just outside of the Karst Terrane defined by the Hays County HCP, so the extent of the final KFR has been broadened to incorporate these features. Also, small areas not defined as karst terrane by Zara Environmental (2008) that are surrounded by karst terrane (e.g. white areas within Edwards north of the Blanco shown in figure 5) have been included in the final North Edwards KFR. This is due to the fact that the karst terranes were derived directly from mapped outcrops of major karst forming limestone, and minimal consideration was given to vertical extents of these limestones. It is likely that even though a karst forming limestone may have some thickness of younger non-karst forming rock above, caves and troglobite habitat exist in these areas.

There are currently four rare species known from the North Edwards KFR, two of which are aquatic. These are *Stygobromus balconis* and a North Edwards KFR endemic salamander-*Eurycea* sp. (nana/sosorum). This particular taxon, known only from two sites in Hays County, is somewhat of an enigma and is awaiting further analyses for taxonomic clarification (Zara 2008, Bendik 2006). The two remaining rare species known from this KFR are the harvestman *Texella mulaiki* (found in all Hays County KFRs except Western Hays), and another North Edwards endemic, the ground beetle *Rhadine* sp. c.f. *austinica*, known from this area and also in Travis County.



**Figure 8.** Intermediate KFR map showing karst terrane extents divided into separate geologically derived units. The karst terrane in the northern tip of Hays County was not included in the intermediate KFR analysis due to the lack of known localities for rare species.



Figure 9. Map of Hays County Karst Fauna Regions.



Figure 10. Geologic cross-section of Hays County showing Karst Fauna Region zones.

# The Western Hays KFR

The Western Hays KFR includes areas with Lower Glen Rose Limestone, isolated outcrops of lower Edwards Group limestone located directly above the Glen Rose, and portions of Upper Glen Rose Limestone found between these rock units. The Blanco River is the southern boundary along most of the region, before shifting to the county line for the southwestern boundary. The northern boundary includes a buffer generally around the extent of Lower Glen Rose Limestone and Edwards Group outlier outcrops to near Onion Creek. The eastern

boundary with the North Edwards KFR connects back to the Blanco River in an area with no known karst species localities.

Nine rare species are found in the Western Hays KFR, three of which are endemic. Two of these are beetles (*Batrisodes grubbsi* and *Rhadine insolita*) and a neoleptonetid spider (*Neoleptoneta* n. sp. 1). Each of these three species is known only from one locality.

## The Bat Cave Fault Block KFR

The Bat Cave Fault Block is comprised of primarily Edwards/Georgetown Limestone, and a portion of Upper Glen Rose Limestone south of the Blanco River. The northern boundary is the Blanco River, merging into the southwestern county line. The southeastern boundary is the Bat Cave Fault, a major normal fault with over 150 feet of vertical displacement (Johnson and Schindel 2008). This fault continues along a northeastern strike, intersecting the Blanco River.

The Bat Cave Fault Block KFR has the second highest number of endemic species in the county after the San Marcos KFR. Of the 14 rare species records there, 7 are endemic. Five of these are terrestrial troglobites.

#### The San Marcos KFR

The northwestern boundary is the Bat Cave Fault Block, extending to the county line along the southwest. The southeastern boundary extends near the limit of the Edwards/Georgetown Limestone, encompassing a small buffer area and areas surrounded by this karstic limestone up to the Blanco River, which serves as the northeastern boundary. The northeastern boundary is the Blanco River up to the intersection of the Bat Cave Fault. This region includes geologic strata of the Hueco Springs, Comal Springs, and Artesian Fault Blocks.

The San Marcos KFR includes the greatest number of endemic karst species among the karst regions in Hays County. Of 28 recorded rare species, 24 are endemics found nowhere else worldwide. Most of these are aquatic species known from three sites that have arguably received some of the most intensive collection efforts for any species of troglobites in the state: Ezell's Cave, San Marcos Springs, and the Artesian Well (see discussion for more on this sampling).

#### The Pedernales KFR

The Pedernales KFR is located in the northern-most part of Hays County, and primarily includes areas with Lower Glen Rose outcrops. The Pedernales River has deeply incised the limestone here, and the Cow Creek Limestone is exposed along lower levels of the river canyon. The region is isolated from other KRFs by a large area of Upper Glen Rose Limestone, which has been significantly less karstified.

None of the 45 rare species considered in this report are known from this KFR. One species of interest, however, is the salamander, *Eurycea* sp. "pedernales". Identified by Chippindale et al. (2000), it is only known from Hammot's Crossing in an isolated band of Cow Creek Limestone (Figure 3). The species is genetically distinct and geographically isolated from other *Eurycea* salamanders, and is a new species awaiting description.

## Endemism Index (percent of shared species method)

The endemism index value calculated for four of the Hays karst faunal regions is depicted in Figure 11. The San Marcos region had the highest value with a score of 50. The Bat Cave Fault Block, although still considerably low, yielded the second highest endemicity value of 10. Seven endemics are known from this region. Both the Western Hays and the North Edwards KFRs produced values under five.



Figure 11. Endemism index: Karst Fauna Regions of Hays County.

# PAE and NDM Analyses

# All Species Data

The "All Species" data set contained 45 species that occurred in 22 cells (Appendix A). TnT stored 16 best trees after 97,216 rearrangements. The consensus trees generated from the 16 best trees (Figures 12, 13) and NDM (Figure 14) chose the same set of three cells (A6-6, A6-7, A6-8) as the areas of highest endemicity. However, the two methods identified different species as endemic (Table 2).



**Figure 12.** Strict Consensus Tree (left) and Majority Rule (50%) Consensus Tree for "All Species" generated using TnT. Trees were derived from 16 best trees generated after 97,216 rearrangements. The selected cells were interpreted as the areas of endemism.



**Figure 13.** Synapomorphies common to all most Parsimonious Trees using "All Species". The selected cells were interpreted as the areas of endemism.

The only area of endemism identified by NDM had a score of 14.330; 17 species were identified as being endemic endemic to the area (Figure 14). Different areas of endemism can have different sets of species. So, the inclusion of more than one area of endemism will result in the representation of more endemic species than in any single one of them. In this case, NDM identified only one area with a score greater than 2. Given the large difference (more than seven-fold) in the score of the identified area and any other potential area, no other areas of endemism with a score less than 2 were identified as such in this analysis.



**Figure 14.** Area of Endemism determined by NDM using "All Species". Of 285 areas examined, the area in blue was the only one with a score of >2 (E = 14.330). Twenty-eight species were present in the area and 17 contributed to the score.

Species #	SPECIES	Endemic species in the area of endem	
used in TnT and NDM		PAE	NDM
0	Allotexiweckelia hirsuta	•	
1	Arrhopilites texensis		
2	Artesia subterranea		•
3	Batrisodes grubbsi		
4	Calathaemon holthuisi		•
5	Cicurina ezelli	•	
6	Cicurina russelli		
7	Cicurina ubicki	•	
8	Comaldessus stygius		
9	Eidmanella n. sp.		•
10	Eurycea nana	•	
11	Eurycea pterophila		
12	Eurycea rathbuni	•	•
13	Eurycea robusta	•	
14	Eurycea sp. federally listed (nana/sosorum)	•	
15	Haideoporus texanus	•	
16	Heterelmis comalensis	•	
17	Holsingerius samacos	•	
18	Lirceolus smithii		•
19	<i>Mooreobdella</i> n.sp.	•	•
20	Neoleptoneta eyeless n. sp.?		
21	Neoleptoneta n. sp. 1		
22	Neoleptoneta n. sp.2		
23	Palaemonetes antrorum		•
24	Phreatodrobia micra		•
25	Phreatodrobia plana		•
26	Phreatodrobia punctata	•	
27	Phreatodrobia rotunda		•
28	Rhadine insolita		
29	Rhadine n. sp. 2 (subterranea group)	•	•
30	Rhadine sp. [subterranea group] eyed		
31	Rhadine sp. cf. austinica		
32	Seborgia relicta		•
33	Sphalloplana mohri		•
34	Stygobromus balconis		
35	Stygobromus flagellatus	•	•
36	Stygoparnus comalensis		

**Table 2.** Endemic species in the areas of endemism using "All Species" data.Dots indicate which species are designated as endemic by PAE and NDM.

Species #	SPECIES	Endemic species in the area of endemism		
used in TnT and NDM		PAE	NDM	
37	Tartarocreagris grubbsi			
38	Tethysbaena texana	•	•	
39	Texella diplospina			
40	Texella grubbsi			
41	Texella mulaiki	•		
42	Texella renkesae	•		
43	Texiweckelia texensis	•	•	
44	Texiweckeliopsis insolita		•	

## Modified Species Data

As a result of the grouping of all *Cicurina* species as *Cicurina bandida*, the modified species data set contained 43 species that occurred in 27 cells (Appendix A). TnT stored 100 most parsimonious trees after 878,120 rearrangements. The consensus trees generated from the set of 100 best trees included the same three (A6-6, A6-7, A7-6) cells that NDM (Figure 14) chose as the most endemic area in the region.

#### Terrestrial Species

The "Terrestrial" data set contained 18 species that occurred in 14 cells (Appendix A). TnT stored 40 most parsimonious trees after 59,165 rearrangements. The result of the consensus trees (Figures 15 and 16) agree with that of NDM (Figure 17). NDM, however, identified three areas of endemism with scores above 1 (Table 3).



**Figure 15.** Strict Consensus Tree (left) and Majority Rule (50%) Consensus (right) for "Terrestrial Species" generated using TnT. The selected cells were interpreted as the areas of endemism.

A_out
A8 5
→ <u></u>
A6_6
6- A6_4
3,8,11 A6 2
14- A5 5
7- A4 1
A3 6
A3 3
17- A3 2
1,2,9 A3_1
A1 7
r2,17 A7 6
11/ 0

**Figure 16.** Synapomorphies common to all trees derived using "Terrestrial Species". The selected cells were interpreted as the areas of endemism.

**Table 3.** Endemic species in the areas of endemism using "Terrestrial Species". These results are for the area depicted in Figure 19 (with the highest score of all three areas, E = 1.75). The dots indicate which species are designated as endemic by PAE and NDM.

Species #	SPECIES	Endemic species in the area of endemism			
used in TnT and NDM		PAE	NDM		
0	Arrhopilites texensis				
1	Batrisodes grubbsi				
2	Cicurina ezelli	•			
3	Cicurina russelli				
4	Cicurina ubicki				
5	<i>Eidmanella</i> n. sp. •				
6	Neoleptoneta eyeless n. sp.?				
7	Neoleptoneta n. sp. 1				
8	Neoleptoneta n. sp.2				
9	Rhadine insolita				
10	Rhadine n. sp. 2 (subterranea group)		•		
11	Rhadine sp. [subterranea group] eyed				
12	Rhadine sp. cf. austinica				
13	Tartarocreagris grubbsi				
14	Texella diplospina				
15	Texella grubbsi				
16	Texella mulaiki				
17	Texella renkesae	•			



**Figure 17.** Areas of endemism (map 1 of 3) determined by NDM using "Terrestrial Species". A total of 104 areas were examined and three had a score > 0.10. Ten species were present in the area and two contributed to the score (E = 1.666).



**Figure 18.** Areas of endemism (map 2 of 3) determined by NDM using "Terrestrial Species". A total of 104 areas were examined and three had a score > 0.10. Eight species were present in the area and two contributed to the score (E = 1.666).



**Figure 19.** Areas of endemism (map 3 of 3) determined by NDM using "Terrestrial Species". A total of 104 areas were examined and three had a score > 0.10. Six species exist in the area and two species contributed to the score (E = 1.750).

#### Modified Terrestrial Species

The "Modified Terrestrial" data set contained 16 species that occurred in 20 cells (Appendix A). TnT stored 20 most parsimomious trees after 81,390 rearrangements. The results of TnT (Figures 20 and 21) agree with that of NDM (Figures 22 and 23) for this data set. NDM, however, identified two areas of endemism with scores above 1 (Table 4).



**Figure 20.** Strict Consensus Tree (left) and Majority Rule (50%) Consensus Tree (right) for "Modified Terrestrial Species" generated using TnT. The selected cells were interpreted as the areas of endemism.



**Figure 21.** Synapomorphies common to all trees derived using "Modified Terrestrial Species". The selected cells were interpreted as the areas of endemism.



**Figure 22.** Areas of endemism determined by NDM using "Modified Terrestrial Species". A total of 103 areas were examined and two had a score > 0.10 Nine species exist in the area and two species contributed to the score (E = 1.666).



**Figure 23.** Areas of endemism determined by NDM using "Modified Terrestrial Species". A total of 103 areas were examined and two had a score > 0.10. Five species exist in the area and two species contributed to the score (E = 1.750).

**Table 4.** Endemic species in areas of endemism using "Modified Terrestrial Species". These results are for the area depicted in Figure 23 (with the highest score among the two areas, E = 1.75). The dots indicate which species are designated as endemic by PAE and NDM.

Species # used	SPECIES	Endemic species in the area of endemism		
in ThT and NDM		PAE	NDM	
0	Arrhopilites texensis			
1	Batrisodes grubbsi			
2	Cicurina bandida			
3	<i>Eidmanella</i> n. sp.	•	•	
4	Neoleptoneta eyeless n. sp.?			
5	Neoleptoneta n. sp. 1			
6	Neoleptoneta n. sp.2			
7	Rhadine insolita			
8	Rhadine n. sp. 2 (subterranea group)	•	•	
9	Rhadine sp. [subterranea group] eyed			
10	Rhadine sp. cf. austinica			
11	Tartarocreagris grubbsi			
12	Texella diplospina			
13	Texella grubbsi			
14	Texella mulaiki			
15	Texella renkesae	•		

## Aquatic Species

The "Aquatic" data set contained 27 species that occurred in 15 cells (Appendix A). TnT stored 16 trees after 34,027 rearrangements. The consensus trees (Figures 24 and 25) and NDM (Figure 26) identified the same set of cells as the areas of endemism (Table 5). Unlike terrestrial species, the aquatic species are highly endemic to these three grid cells. Because of this, the only area of endemism with score > 2 identified by NDM had a score of 13.330.



**Figure 24.** Strict Consensus Tree (left) and Majority Rule (50%) Consensus Tree (right) for "Aquatic Species" generated using TnT. The selected cells were interpreted as the areas of endemism.



**Figure 25.** Synapomorphies common to all trees using "Aquatic Species". The selected cells were interpreted as the areas of endemism.



**Figure 26.** Areas of endemism determined by NDM using "Aquatic Species". Of 36 areas examined. This figure depicts the only area that received a score greater than 2 (E = 13.330). Twenty-three species exist in the area and 15 contributed to the score.

Species #	SPECIES	Endemic species in the area of ender	
used in ThT and NDM		PAE	NDM
0	Allotexiweckelia hirsuta	•	
1	Artesia subterranea		•
2	Calathaemon holthuisi		•
3	Comaldessus stygius		
4	Eurycea nana	•	
5	Eurycea pterophila		
6	Eurycea rathbuni	•	•
7	Eurycea robusta	•	
8	Eurycea sp. federally listed (nana/sosorum)		
9	Haideoporus texanus	•	
10	Heterelmis comalensis	•	
11	Holsingerius samacos	•	
12	Lirceolus smithii		•
13	Mooreobdella n.sp.	•	•
14	Palaemonetes antrorum		•
15	Phreatodrobia micra		•
16	Phreatodrobia plana		•
17	Phreatodrobia punctata	•	
18	Phreatodrobia rotunda		•
19	Seborgia relicta		•
20	Sphalloplana mohri		•
21	Stygobromus balconis		
22	Stygobromus flagellatus	•	•
23	Stygoparnus comalensis		
24	Tethysbaena texana	•	•
25	Texiweckelia texensis	•	•
26	Texiweckeliopsis insolita		•

**Table 5.** Endemic species in areas of endemism using "Aquatic Species". The dots indicate which species are designated as endemic by PAE and NDM.

## Discussion

During our assessment of methods for creating management units for cave species, we accrued a list of pros and cons for different methods, and provide a review of that here. In addition to the methods we used in this county, we review and discuss genetic data from this county and others as another source of data from which to create karst fauna regions.

#### Karst Fauna Regions

In our effort to use similar techniques to those used in Travis, Williamson and Bexar counties to create Karst Fauna Regions, we determined the primary advantage of the method is that it has a focus on habitat continuity, and allows for the integration of multiple datasets (biogeographic, geologic, endemism). Habitat continuity is commonly used as a factor for creating endangered species management units (USFWS 1991 and 1992). Using habitat continuity makes sense when considering the use of these area delineations. For example, it may be determined that in order to downlist an endangered species, at least five populations in each management area need to be preserved, or it may be determined that harm to endangered species that results from development activities needs to be mitigated within the same management unit. These decisions are likely made with the consideration of potential migration within the management unit and preservation of within-species genetic diversity among management units.

The method also allows for integration of multiple datasets. In the case of our creation of the San Marcos KFR, the number of aquatic endemics was so compelling that we reevaluated the geologic information and created a unique KFR ("splitting") to reflect that information. In the case of the Georgetown/Edwards outliers in the central portion of the county, we had only two records of widespread species there, so we made a decision to lump those formations into the nearby Western Hays KFR in order to reflect the continuity of aquatic habitat.

There are many downsides to this method, as well. It is subjective and iterative, therefore not precisely repeatable. If the same dataset were provided to a different set of biogeographers, they would likely find a different solution than we did. Except in the cases where we have data-rich sites (e.g. San Marcos Springs area), decisions about lumping or splitting regions were often based on few species with few locality records. The criteria for making those decisions were different depending on the taxon involved, largely because of differences in habitat requirements (e.g. aquatic vs. terrestrial). One might also expect that differences in phylogenetic history would lead to different patterns of biogeography, as with aquifer adapted cirolanid vs. asellid isopods in Texas (Krejca 2005). Contributing to this problem is the lack of sampling in some regions which greatly affects the outcome of the map.

Essentially the only KFR we created that is strongly supported by repeatable techniques is the San Marcos KFR. There are many endemic species in that region, and both a qualitative examination of the range maps and the statistically rigorous endemicity analyses (PAE and NDM) supported this region. The other regions are weakly supported by only qualitative examination.

## Endemicity analyses

We performed endemicity analyses using three methods. The first, percentage of shared species, showed graphically the high amount of endemism in the San Marcos KFR. The three other KFRs all yielded low values (ten or below) despite the presence of some endemic species. This method is part of the iterative procedure as per the discussion on KFRs above. As such, it has many of the pros and cons of that method. It is a subjective *post hoc* analysis because the regions are determined first by examination of both the geology and species range maps. Endemicity is then calculated for each region. It is common in biogeographic studies to perform such analyses, however clearly the results are somewhat pre-determined based on the user-defined input. The advantage is that it has the "human

touch" of being able to see both strong and weak patterns, but it also has the disadvantage of a lack of statistic rigor and repeatability.

The area results of the PAE and NDM were almost always identical. In the few cases in which discrepancies appeared, areas of endemism determined by NDM included one or two cells beyond those selected by the PAE. In general, the areas of highest endemism across the data sets include three 5 km x 5 km cells (A6-6, A6-7 and A7-6 on Figures 14 and 26), and this area of endemism proved to be remarkably robust in this analysis.

The PAE and NDM identified different species as endemic for each of the five data sets. However, the species identified as endemic depend critically on the exact form of the PAE and the objective function of NDM. Consequently, results can be artefactual and must be treated with caution.

Aquatic species of the region have the highest relative representation and endemicity in the area of endemism (Figure 26). Aquatic species contribute 93% of the endemicity score to the areas selected for the "All Species" and "Modified Species" data sets. Representation and endemism is much lower for terrestrial species. However, this does not imply that the terrestrial species themselves are less endemic but rather that the selected areas of endemism for terrestrial species contain relatively few species because terrestrial endemic species are distributed across the landscape.

Clearly the advantage of these two methods is that they are extremely robust. The selection of regions of endemicity is as close to a 'blind' process as is possible, the process is repeatable and creates answers with numeric values and testable results. While the results of this method are clearly valid, a potential problem is in the interpretation. The results of this method created only one area of endemicity as a result of the input data (vs. the five areas described above). Our knowledge of the history of sampling is that the effort in this area is exceedingly high compared to other areas in the county. San Marcos Springs is the locality for several endangered species and receives significantly more biological surveys than other springs in Hays County. The Artesian Well on Texas State University (TSU) campus has been intensively sampled for decades (e.g. Holsinger and Longley 1980). The terrestrial fauna at Wonder World Drive are better sampled than any other area in the county (Veni 2002) and Ezell's Cave has received more visits by biologists than any other cave in the state (Krejca and Gluesenkamp 2007). Therefore we interpret this single area of endemicity to be at least partially associated with unequal sampling. The downsides of using this method are that only one dataset is used (biological) and therefore biases in that dataset (e.g. unequal sampling) are reflected in the results. It also does not take into account habitat continuity, for example while the endemic species are known from three cells, the geology might be the same in neighboring cells that are undersampled.

#### Genetic analyses

Genetic analyses were not performed within the scope of this project, but genetic data are being collected rapidly and several studies exist on species in Hays County. It is a valid technique for biogeography, therefore we discuss it here. Genetic studies have many advantages in terms of defining management units: in many cases they are data rich (e.g. genes with many base pairs of information), the methods are scientifically defensible and statistically rigorous. The downside is that after a tree is created, there is a common step performed that involves *post-hoc* interpretation to create hypotheses about vicariant events that lead to the tree. Few researchers perform statistical tests of trees (e.g. Hillis et al. 1996, Huelsenbeck et al. 1996). When Krejca (2005) tested the gene trees of cave species against a logical null hypothesis, simple geographic distance, she was not able to disprove the null. It is possible that many gene trees are no more geographically informative for among-population relatedness than a simple map of distance. This demonstrates that it is easy to over-interpret phylogenetic trees. Because of this problem, and also because genes track historic population connections and not the modern ability of individuals to repopulate disjunct areas, we support the use of these methods only in combination with assessments of modern habitat continuity.

#### Recommendations

Delineating endangered species recovery regions is not a simple task. No single method is supported in this study; instead the intent is to point out obvious characteristics: the use of different methods yields different results. When charged with this task, a recommendation is made clearly defining those methods at every step and making the reasoning behind each decision transparent. When there is a choice between two similar methods at some stage, it is ideal to use both and evaluate the differences in results. If the differences in scale are minor (e.g. in our study between PAE and NDM), this lends confidence to the results. In this study, the difference between using the iterative method and the PAE/NDM method was major: the first created five KFRs and the second created only a single area of endemism. In this case the purpose of the subdivisions needs to be assessed in order to be certain that the right method is used.

For delineating regions for cave fauna conservation, methods that include at least some component of a habitat-based solution are supported, and are not totally dependent on biological data. The reasoning is that cave conservation needs to proceed reasonably conservatively because caves cannot be "re-grown" and karst habitat is not easily remediated. In the case of genetically or morphologically identical populations on either side of a divide that is entirely non-karstic, a conservative approach is to use the evolutionary species concept. In this case the assumption would be that the two populations could not exchange genes in the future therefore they are treated as independent. In the case of no species records in a karst region, a recommendation is made which assumes that the sampling effort is not complete, therefore species may be present. The iterative process we employed here uses geologic information to make hypotheses about potential species occupation.

Creating a single map that represents many species is obviously complex. In the case where many explicit decisions need to be made about specific Hays County karst species, we suggest that a different map is needed for each species. The obvious complexity with our dataset is that we incorporate both terrestrial and aquatic species. However even within groups of species that occur in the same habitat there are many reasons to create different biogeographic boundaries. For example the phylogenetic history of each taxon is expected to be different (e.g. Krejca 2005), and many other factors including migration rates, life history strategies, reproduction and even evolution rates may dictate the need to create unique maps for each species.

#### Acknowledgements

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#### Personnel

Dr. Jean Krejca served as the Scientific Coordinator for this project. She also assisted with field surveys, data analysis and wrote portions of this report. She is a subterranean species specialist. Jean has a Bachelor's degree in Zoology, and a Ph.D. in Evolution, Ecology and Behavior from the University of Texas. Her dissertation work focused on cave adapted aquatic fauna, biogeography and hydrology of Texas and North Mexico. Since 1991 she has worked as a cave biologist and her experience in that area spans across the United States (Arkansas, California, Texas, Nevada, Illinois, Missouri, Indiana, Tennessee, North and South Carolina) as well as Mexico, Belize, Thailand and Malaysia. Her publication list on these areas is extensive. Texas cave biology experience started in 1997 and includes detailed collections of aquatic cave fauna for research, monitoring for endangered species, and working as a Karst Invertebrate Specialist for the U.S. Fish and Wildlife Service. In 2003 she co-founded Zara Environmental LLC where she continued her work from independent consulting and expanded to perform land management for landowners with endangered species, consult on endangered species permits, and perform custom research projects. In addition she has been involved with a variety of public outreach efforts such as public talks, field trips, and cave biology photography. She holds a USFWS endangered species permit (TE028652-0) and several state permits.

Kathleen O'Connor managed this project, oversaw data compilation and management, coordinated and conducted site visits and wrote portions of the text. Kathleen earned her M.S. in Wildlife Ecology from Texas State University with an emphasis on herpetology. She has over five years of experience working with both endangered birds and karst invertebrates of Central Texas, including extensive work in the Balcones Canyonlands Preserve. Prior to earning her degree, Kathleen completed a USFWS Americorps term at the San Marcos Federal Fish Hatchery and Technology Center, where she gained valuable experience working with several endangered aquatic species, including the Texas Blind Salamander and the San Marcos Salamander. She holds a USFWS endangered species permit # TE227505.

Marcus O. Gary contributed to the geology and geospatial analyses.

Marcus is a hydrogeologist specializing in karst forming processes and the implications that karst geology has on natural resource management. Marcus received an Associate of Science degree in Marine Technology at the College of Oceaneering, a B.S. degree in hydrogeology and environmental geology at the University of Texas, and is currently working on a volcanogenic karst dissertation project at the University of Texas. His research has been internationally recognized for investigating of the world's deepest underwater sinkhole and interpreting the geologic mechanisms that formed the karst system. For eight years he worked in the Texas Water Science Center of the U.S. Geological Survey, performing a multitude of tasks related to water resources. Projects included developing methods to quantify spring flow using acoustic technology, monitoring stage and water chemistry parameters at springs, performing a geochemical investigation of the Barton Springs Segment of the Edwards Aquifer, providing diving support for coring and karst monitoring projects, serving as a dive safety officer for the Central Region, and designing and implementing a variety of continuous monitoring projects at locations across Texas. His work at Zara since 2007 includes geologic assessments, drainage basin delineation, and dye tracing.

Peter Sprouse assisted with coordination of field visits and assisted with biological surveys at several Hays County caves. Mr. Sprouse has extensive experience in karst studies, endangered species, and cartography. He has thirty nine years of expertise exploring and studying caves and a wide knowledge of karst biology, with nine species named in his honor. He has spent many years as a professional contractor conducting karst surveys, biological inventories, and cave mapping in central Texas. The National Speleological Society has given him the prestigious Lew Bicking Award, named him an NSS Fellow, and he was the medal winner in the 1980 and 1986 NSS Cartographic Salons. He holds a USFWS endangered species permit # TE014168-0.

Dr. Sahotra Sarkar and his lab assistants, Kumar Mainali and Blake Sissel of the Biodiversity and Biocultural Conservation Laboratory at University of Texas at Austin, provided all PAE and NDM analyses of the data. Dr. Sahotra Sarkar is a philosophy professor and integrative biologist at the University of Texas at Austin. He is the author of several books and articles about philosophy and science. He earned a BA from Columbia University, and a MA and PhD from the University of Chicago.

Cell					
ID	KFR	Site Name	SPECIES	All	Modified
<b>N A A</b>	San Marcos	Artosian Wall	Allotoviwoskolia birsuta	Species	Species
A0-0 A3-1	Western	Grapevine	Arrhonilites texensis	Terrestrial	Terrestrial
	Hays	Cave		Terrestria	Terrestria
A5-5	Bat Cave FB	Wissman's Sink #2	Arrhopilites texensis	Terrestrial	Terrestrial
A6-6	San Marcos	Artesian Well	Artesia subterranea	Aquatic	Aquatic
A7-6	San Marcos	Ezell's Cave	Artesia subterranea	Aquatic	Aquatic
A3-1	Western Hays	Grapevine Cave	Batrisodes grubbsi	Terrestrial	Terrestrial
A6-6	San Marcos	Artesian Well	Calathaemon holthuisi	Aquatic	Aquatic
A7-6	San Marcos	Ezell's Cave	Calathaemon holthuisi	Aquatic	Aquatic
A6-9	San Marcos	(Rattlesnake Sink?)	Cicurina bandida	Not Included	Terrestrial
A3-6	North	6F Cave	Cicurina bandida	Not	Terrestrial
	Edwards			Included	
A2-7	North	Beyond the	Cicurina bandida	Not	Terrestrial
	Edwards	Pail		Included	_
A7-5	San Marcos	Cave (Ogden 16)	Cicurina bandida	Not Included	Terrestrial
A7-6	San Marcos	Cave (Ogden 17)	Cicurina bandida	Not Included	Terrestrial
A7-6	San Marcos	Cave (Ogden 18)	Cicurina bandida	Not Included	Terrestrial
A7-6	San Marcos	Corrie Smith Cave No. 1	Cicurina bandida	Not Included	Terrestrial
A1-7	North Edwards	County Line Bat Cave	Cicurina bandida	Not Included	Terrestrial
A3-3	Western Hays	Flocke's Cave	Cicurina bandida	Not Included	Terrestrial
A7-5	San Marcos	Formation Cave	Cicurina bandida	Not Included	Terrestrial
A6-6	San Marcos	Freeman Crawl Cave	Cicurina bandida	Not Included	Terrestrial
A5-6	San Marcos	Fritz's Cave	Cicurina bandida	Not Included	Terrestrial
A4-6	North Edwards	Hackberry Cave	Cicurina bandida	Not Included	Terrestrial
A3-1	Western Hays	Harwell's Greenhouse Pit	Cicurina bandida	Not Included	Terrestrial
A1-7	North Edwards	Hays Ranch Bat Cave	Cicurina bandida	Not Included	Terrestrial
A4-6	North Edwards	Hole in the Ground	Cicurina bandida	Not Included	Terrestrial
A2-6	North Edwards	Hoskins Hole	Cicurina bandida	Not Included	Terrestrial
A3-5	Western Hays	Kiwi Sink	Cicurina bandida	Not Included	Terrestrial

**Appendix A.** Table of all rare species data, locality records and karst fauna region in which it occurs.

Cell					
ID	KFR	Site Name	SPECIES	All	Modified
				Species	Species
A3-1	Western Hays	Lost Springs Cave	Cicurina bandida	Not Included	Terrestrial
A3-3	Western Hays	Pucker Cave	Cicurina bandida	Not Included	Terrestrial
A3-6	North Edwards	Sky Ranch Cave	Cicurina bandida	Not Included	Terrestrial
A5-6	San Marcos	Sofa Cave	Cicurina bandida	Not Included	Terrestrial
A2-6	North Edwards	Taylor Bat Cave	Cicurina bandida	Not Included	Terrestrial
A7-5	San Marcos	Twin Entrance Cave	Cicurina bandida	Not Included	Terrestrial
A7-6	San Marcos	Ezell's Cave	Cicurina ezelli	Terrestrial	Not Included
A3-1	Western Hays	Grapevine Cave	Cicurina ezelli	Terrestrial	Not Included
A6-2	Bat Cave FB	Boyett's Cave	Cicurina russelli	Terrestrial	Not Included
A5-5	Bat Cave FB	Fern Cave	Cicurina ubicki	Terrestrial	Not Included
A6-6	San Marcos	McGlothin Sink	Cicurina ubicki	Terrestrial	Not Included
A4-5	Bat Cave FB	Fern Bank Spring	Comaldessus stygius	Aquatic	Aquatic
A7-6	San Marcos	Ezell's Cave	<i>Eidmanella</i> n. sp.	Terrestrial	Terrestrial
A7-5	San Marcos	McCarty Cave	<i>Eidmanella</i> n. sp.	Terrestrial	Terrestrial
A6-6	San Marcos	McGlothin Sink	<i>Eidmanella</i> n. sp.	Terrestrial	Terrestrial
A6-7	San Marcos	San Marcos Springs	Eurycea nana	Aquatic	Aquatic
A4-5	Bat Cave FB	Fern Bank Spring	Eurycea pterophila	Aquatic	Aquatic
A3-1	Western Hays	Grapevine Cave	Eurycea pterophila	Aquatic	Aquatic
A3-3	Western Hays	Jacob's Well	Eurycea pterophila	Aquatic	Aquatic
A5-5	Bat Cave FB	Blanco River Spring	Eurycea pterophila	Aquatic	Aquatic
A4-4	Western Hays	Spring 004	Eurycea pterophila	Aquatic	Aquatic
A3-4	Western Hays	Spring 005	Eurycea pterophila	Aquatic	Aquatic
A2-0	Western Hays	Spring 008	Eurycea pterophila	Aquatic	Aquatic
A5-5	Western Hays	Cypress Creek Spring	Eurycea pterophila	Aquatic	Aquatic
A5-5	Bat Cave Fault Block	Rancho Cima Dam Spring	Eurycea pterophila	Aquatic	Aquatic
A6-6	San Marcos	Artesian Well	Eurycea rathbuni	Aquatic	Aquatic
A7-6	San Marcos	Ezell's Cave	Eurycea rathbuni	Aquatic	Aquatic

Cell	KFR	Site Name	SPECIES	AII	Modified
ID				Species	Species
A7-6	San Marcos	Johnson's Well	Eurycea rathbuni	Aquatic	Aquatic
A7-6	San Marcos	Primer's Well	Eurycea rathbuni	Aquatic	Aquatic
A6-7	San Marcos	Rattlesnake Cave	Eurycea rathbuni	Aquatic	Aquatic
A6-7	San Marcos	San Marcos Springs	Eurycea rathbuni	Aquatic	Aquatic
A6-6	San Marcos	Seep on Sessoms Creek	Eurycea rathbuni	Aquatic	Aquatic
A7-6	San Marcos	Wonder Cave	Eurycea rathbuni	Aquatic	Aquatic
A7-6	San Marcos	Underneath Blanco; I-35	Eurycea robusta	Aquatic	Aquatic
A0-7	North Edwards	Spillar Ranch Springs	Eurycea sp. (nana/sosorum)	Aquatic	Aquatic
A2-6	North Edwards	Stuart Springs	Eurycea sp. (nana/sosorum)	Aquatic	Aquatic
A6-6	San Marcos	Artesian Well	Haideoporus texanus	Aquatic	Aquatic
A6-7	San Marcos	San Marcos Springs	Heterelmis comalensis	Aquatic	Aquatic
A6-6	San Marcos	Artesian Well	Holsingerius samacos	Aquatic	Aquatic
A6-6	San Marcos	Artesian Well	Lirceolus smithii	Aquatic	Aquatic
A6-7	San Marcos	San Marcos Springs	Lirceolus smithii	Aquatic	Aquatic
A6-6	San Marcos	Artesian Well	<i>Mooreobdella</i> n.sp.	Aquatic	Aquatic
A7-6	San Marcos	Ezell's Cave	Mooreobdella n.sp.	Aquatic	Aquatic
A6-7	San Marcos	San Marcos Springs	<i>Mooreobdella</i> n.sp.	Aquatic	Aquatic
A6-4	Bat Cave FB	A.J. Rod Cave	<i>Neoleptoneta</i> eyeless n. sp.?	Terrestrial	Terrestrial
A4-1	Western Hays	Burnett Ranch Cave	<i>Neoleptoneta</i> n. sp. 1	Terrestrial	Terrestrial
A6-2	Bat Cave FB	Boyett's Cave	Neoleptoneta n. sp.2	Terrestrial	Terrestrial
A6-6	San Marcos	Artesian Well	Palaemonetes antrorum	Aquatic	Aquatic
A7-6	San Marcos	Ezell's Cave	Palaemonetes antrorum	Aquatic	Aquatic
A7-6	San Marcos	Johnson's Well	Palaemonetes antrorum	Aquatic	Aquatic
A7-6	San Marcos	Wonder Cave	Palaemonetes antrorum	Aquatic	Aquatic
A6-6	San Marcos	Artesian Well	Phreatodrobia micra	Aquatic	Aquatic
A6-7	San Marcos	San Marcos Springs	Phreatodrobia micra	Aquatic	Aquatic
A6-6	San Marcos	Artesian Well	Phreatodrobia plana	Aquatic	Aquatic
A6-7	San Marcos	San Marcos Springs	Phreatodrobia plana	Aquatic	Aquatic
A6-7	San Marcos	San Marcos Springs	Phreatodrobia punctata	Aquatic	Aquatic
A6-6	San Marcos	Artesian Well	Phreatodrobia rotunda	Aquatic	Aquatic
A6-7	San Marcos	San Marcos Springs	Phreatodrobia rotunda	Aquatic	Aquatic

Cell	KFR	Site Name	SPECIES	All	Modified
ID				Species	Species
A3-1	Western Hays	Grapevine Cave	Rhadine insolita	Terrestrial	Terrestrial
A7-6	San Marcos	Ezell's Cave	<i>Rhadine</i> n. sp. 2 (subterranea group)	Terrestrial	Terrestrial
A6-7	San Marcos	Finger Cave	Rhadine n. sp. 2 (subterranea group)	Terrestrial	Terrestrial
A7-5	San Marcos	McCarty Cave	<i>Rhadine</i> n. sp. 2 (subterranea group)	Terrestrial	Terrestrial
A6-2	Bat Cave FB	Boyett's Cave	<i>Rhadine</i> sp. [subterranea group] eyed	Terrestrial	Terrestrial
A1-7	North Edwards	Dahlstrom Cave	Rhadine sp. cf. austinica	Terrestrial	Terrestrial
A3-6	North Edwards	Michaelis Cave	Rhadine sp. cf. austinica	Terrestrial	Terrestrial
A6-6	San Marcos	Artesian Well	Seborgia relicta	Aquatic	Aquatic
A7-6	San Marcos	Ezell's Cave	Seborgia relicta	Aquatic	Aquatic
A6-6	San Marcos	Artesian Well	Sphalloplana mohri	Aquatic	Aquatic
A7-6	San Marcos	Ezell's Cave	Sphalloplana mohri	Aquatic	Aquatic
A6-2	Bat Cave FB	Boyett's Cave	Stygobromus balconis	Aquatic	Aquatic
A5-5	North Edwards	Autumn Woods Well	Stygobromus balconis	Aquatic	Aquatic
A6-6	San Marcos	Artesian Well	Stygobromus flagellatus	Aquatic	Aquatic
A7-6	San Marcos	Ezell's Cave	Stygobromus flagellatus	Aquatic	Aquatic
A6-7	San Marcos	Rattlesnake Cave	Stygobromus flagellatus	Aquatic	Aquatic
A6-7	San Marcos	San Marcos Springs	Stygobromus flagellatus	Aquatic	Aquatic
A4-5	Bat Cave FB	Fern Bank Spring	Stygoparnus comalensis	Aquatic	Aquatic
A3-3	Western Hays	Wimberley Bat Cave	Tartarocreagris grubbsi	Terrestrial	Terrestrial
A5-5	Bat Cave FB	Wissman's Sink	Tartarocreagris grubbsi	Terrestrial	Terrestrial
A6-6	San Marcos	Artesian Well	Tethysbaena texana	Aquatic	Aquatic
A7-6	San Marcos	Ezell's Cave	Tethysbaena texana	Aquatic	Aquatic
A6-7	San Marcos	San Marcos Springs	Tethysbaena texana	Aquatic	Aquatic
A5-5	Bat Cave FB	Ladder Cave	Texella diplospina	Terrestrial	Terrestrial
A4-1	Western Hays	Burnett Ranch Cave	Texella grubbsi	Terrestrial	Terrestrial
A5-5	Bat Cave FB	Wissman's Sink	Texella grubbsi	Terrestrial	Terrestrial
A5-5	Bat Cave FB	Wissman's Sink #2	Texella grubbsi	Terrestrial	Terrestrial
A8-5	San Marcos	Big Mouth Cave	Texella mulaiki	Terrestrial	Terrestrial
A7-6	San Marcos	Ezell's Cave	Texella mulaiki	Terrestrial	Terrestrial
A5-5	Bat Cave FB	Fern Cave	Texella mulaiki	Terrestrial	Terrestrial
A5-5	Bat Cave FB	Ladder Cave	Texella mulaiki	Terrestrial	Terrestrial
A7-5	San Marcos	McCarty Cave	Texella mulaiki	Terrestrial	Terrestrial

Cell I D	KFR	Site Name	SPECIES	All Species	Modified Species
A6-6	San Marcos	McGlothin Sink	Texella mulaiki	Terrestrial	Terrestrial
A3-6	North Edwards	Michaelis Cave	Texella mulaiki	Terrestrial	Terrestrial
A7-5	San Marcos	Pulpit Cave	Texella mulaiki	Terrestrial	Terrestrial
A5-5	Bat Cave FB	Root Beard Cave	Texella mulaiki	Terrestrial	Terrestrial
A7-6	San Marcos	Tricopherous Cave	Texella mulaiki	Terrestrial	Terrestrial
A7-6	San Marcos	Ezell's Cave	Texella renkesae	Terrestrial	Terrestrial
A3-2	Western Hays	Magens Sink	Texella renkesae	Terrestrial	Terrestrial
A6-6	San Marcos	Artesian Well	Texiweckelia texensis	Aquatic	Aquatic
A7-6	San Marcos	Ezell's Cave	Texiweckelia texensis	Aquatic	Aquatic
A6-7	San Marcos	San Marcos Springs	Texiweckelia texensis	Aquatic	Aquatic
A6-6	San Marcos	Artesian Well	Texiweckeliopsis insolita	Aquatic	Aquatic
A6-7	San Marcos	San Marcos Springs	Texiweckeliopsis insolita	Aquatic	Aquatic