Karst Invertebrate
Habitat Requirements

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1.0 INTRODUCTION

Sixteen karst invertebrate species are listed as endangered in central Texas. Nine of these species occur in Bexar County and seven occur in Travis and/or Williamson counties (Table 1).

For more information on these species, see the Recovery Plan for Endangered Karst Invertebrates in Travis and Williamson Counties (Service 1994) and the Bexar County Karst Invertebrates Recovery Plan (Service 2011).

All of these invertebrates are troglobites, which means they spend their entire lives underground. The purpose of this document is to provide information on the habitat requirements of these species.

Table 1. Endangered Karst Invertebrates in central Texas

County	Common Name	Scientific Name
Bexar	no common name	*Rhadine exilis*
Bexar	no common name	*R. infernalis*
Bexar	Helotes mold beetle	*Batrisodes venyivi*
Bexar	Cokendolpher cave harvestman	*Texella cokendolpheri*
Bexar	Government Canyon Bat Cave spider	*Tayshaneta microps*
Bexar	Robber Baron Cave meshweaver	*Cicurina baronia*
Bexar	Madla Cave meshweaver	*C. madla*
Bexar	Braken Bat Cave meshweaver	*C. venii*
Bexar	Government Canyon Bat Cave meshweaver	*C. vespera*
Travis	Tooth Cave spider	*Tayshaneta myopica*
Travis	Tooth Cave pseudoscorpion	*Tartarocreagris texana*
Travis	Bee Creek Cave harvestman	*Texella reddelli*
Travis	Kretschmarr Cave mold beetle	*Texamaurops reddelli*
Travis/Williamson	Tooth Cave ground beetle	*Rhadine persephone*
Travis/Williamson	Bone Cave harvestman	*Texella reyesi*
Williamson	Coffin Cave mold beetle	*Batrisodes texanus*

2.0 HABITAT REQUIREMENTS

2.1 Adaptation to the Cave Environment

2.1.1 Retreat to the subsurface

During the course of climatic changes two million to ten thousand years ago, certain creatures retreated into the more stable cave environments, while their respective surface relatives either emigrated or became extinct (Barr 1968, Elliott and Reddell 1989). Exploitation of cave environments for temporary or seasonal shelter is common among many surface-dwelling organisms, but this alone would probably not result in sufficient isolation among surface and subsurface populations for speciation to occur. Some of these ancestors may have been pre-adapted to living in cave environments (K. Lavoie, State University of New York, pers. comm. 2008). However, long-term occupation of subsurface environments during periods of climate change (for example, Pleistocene glaciations) is a plausible hypothesis for the evolution of troglobitic taxa in central Texas (White 2006). In this scenario, some populations may persist in relatively mild and stable cave environments during periods of climate change, while surface populations are forced to migrate to more suitable climates or face extinction. This hypothesis leads to vicariance (speciation by geographic isolation) and is supported by several lines of evidence (Barr 1968). Subsequent changes to subsurface habitats, for example, fragmentation and isolation due to erosion or faulting, may lead to further speciation among troglobitic taxa (Elliott and Reddell 1989, Veni 1994). In addition, this cycle may repeat over time, with multiple invasions of subsurface habitat by surface species (Cokendolpher 2004, White 2006).

Just as relative dates can be established for geologic events, mitochondrial deoxyribonucleic acid (mtDNA) can establish relative dates for the isolation of closely related species or populations from their common ancestor. Among the listed invertebrates, the *Cicurina* have received phylogeographic study (study of historic relationships that may be responsible for current geographic ranges of species) (White 2006, White et al. 2009). White (2006) and White et al. (2009) found that diversity among troglobitic *Cicurina* was the product of the progressive availability of karst habitat that was exposed to the surface due to water eroding the soil as it recharged the aquifer below over the past 10 million years. These studies demonstrated a strong correlation between *Cicurina* genetic diversity and the timing of geologic processes of the Balcones Escarpment.

2.1.2 Cave Formation

To understand cave habitat and how it affects the ecology and life history (a species' life cycle) of troglobites, it is essential to consider the origin of karst features. Some are formed above the water table (vadose) and others form below (phreatic). Many caves have a history of both phreatic and vadose development, with initial phreatic development and subsequent vadose downcutting. Many details of cave formation are important to the understanding of modern surface and subsurface drainage basins, a critical feature for karst invertebrate habitat preservation.

Physical characteristics of caves vary significantly and influence the habitat for karst-dwelling species. These characteristics are determined by cave genesis and subsequent geologic evolution. For example, many caves are discrete from one another because the strata containing them are dissected and isolated due to stream downcutting and/or faulting. This isolation presents a barrier to troglobite interaction and leads to the evolution of many endemics (species restricted to a particular geographic area, such as a single cave). The configuration of a cave entrance may constrain nutrient and airflow. Some cave entrances are very small, which limits nutrient input; whereas, other entrances are very large, which provides more opportunity for nutrients to enter the ecosystem. In the former case, only taxa adapted to the lowest energy situation exist there, and in the latter case the cave may contain a high diversity of surface-dwelling organisms. These physical characteristics are partially responsible for species composition and contribute to differences among caves.

2.1.3 Physical Adaptations and Life History of Cave Life

Physical factors in caves that influence karst invertebrate evolution include 1) the absence of sunlight, which prohibits plant growth and results in low nutrient levels and 2) a stable environment with uniform temperatures and high humidity. These parameters favor the evolution of troglomorphic characteristics including reduction or loss of eyes and pigment, enhancement of sensory structures such as longer limbs, and life history strategies with low metabolic and reproductive rates (Poulson and White 1969, Howarth 1983, Culver 1986, Culver et al. 1995, Jeffery 2001). Similarities in selective pressures in caves transcend geography, resulting in convergent evolution reflected in high levels of morphological similarity among troglobites (Protas et al. 2006).

The life span of troglobites is typically long relative to that of related surface species. Average life spans of the listed troglobitic invertebrates in central Texas are unknown, but are likely multiple years for some species (for example, *Cicurina* spp.), based on observations of juveniles kept in captivity (Bennett 1985, Cokendolpher 2004, Veni and Associates 2008).

2.2 Habitat Requirements

The habitat of these species includes karst limestone caves and mesocaverns (humanly impassable voids described below). Within this habitat, these animals depend on high humidity, stable temperatures, and surface-derived nutrients including leaf litter, animal droppings, and animal carcasses. While these species spend their entire lives underground, their ecosystem is dependent on the overlying surface habitat (see the nutrient discussion below).

2.2.1 Cave and Karst Habitat

Terminology specific to cave and karst habitat is not commonly used in other environments, so special treatment is given here. The term “karst” refers to a type of terrain that is formed by the slow dissolution of calcium carbonate from limestone bedrock by mildly acidic groundwater (Veni and Associates 2008). This process creates numerous cave openings, cracks, fissures, fractures, and sinkholes that resemble Swiss cheese. Caves are typically defined as naturally occurring voids traversable to a certain extent by humans. The Texas

Speleological Survey (2011) (http://www.txspeleologicalsurvey.org) defines a cave as: "[In Texas], a cave is any natural occurring, humanly passable subsurface cavity which is at least 5 meters (m) (16 feet (ft)) in traverse length, and where no dimension of the entrance exceeds the length." In many cases, cave entrances are transient with surface erosion causing collapses and infilling. Curl (1958) has proposed that most (perhaps 10 times as many) cave-sized passages in limestone do not have entrances large enough for human entry. These entranceless caves may lack surface expression, or, if they approach the surface, they can collapse and be expressed as sinkholes. Sinkholes and other karst features in Texas are commonly small and difficult to detect (Veni 2001). For the purposes of karst invertebrate recovery it is important to consider all karst features that may contain habitat, including voids that are too small to be humanly passable. These voids are sometimes referred to as interstitial spaces (Veni 1994), but because this term is frequently used in association with submerged gravel streambeds in non-karst areas, this document will use the term "mesocaverns." Mesocaverns are inaccessible spaces extending from the walls of a cave passage, or may exist farther from a cave in an area not accessible from a cave passage. For more information on mesocaverns see the mesocavern subsection below.

2.2.2 Mesocaverns

Mesocavernous voids provide important sheltering habitat for karst invertebrates. During temperature extremes, small mesocavernous spaces may have a physical environment with more favorable humidity and temperature levels than the larger caves passage (Howarth 1983). Troglobites may spend the majority of their time in such retreats, only leaving them during temporary forays into the larger cave passages to forage (Howarth 1987). Human access to mesocaverns is limited; therefore, data about invertebrate use of mesocaverns is limited. Scientists have hypothesized that the majority of nutrients are located in humanly accessible portions of terrestrial caves with open entrances (Culver and Pipan 2009), and for this reason they are believed to be the foci of troglobitic populations that may occur in low densities throughout the karst. However, because metabolic rates of troglobites are typically low, they may be able to sustain periods ranging from months to years existing on lower levels of food or no food in mesocaverns (Howarth 1983).

Several studies indicate that mesocaverns outside of known occupied caves are used by karst invertebrates. The only way to sample these locations is via bedrock excavation. For example, central Texas endangered karst invertebrates have been found in caves that immediately prior to sampling had no human entrance (Veni and Associates 2008), and they have been found in holes drilled into the karst that intersect mesocaverns near caves. For example, at the Lakeline Mall in Williamson County, Texas, boreholes were drilled to determine the presence of karst invertebrates in mesocaverns adjacent to two caves occupied by listed species (*Rhadine persephone* and *Texella reyesi*). *Rhadine persephone* (a species of the same genus as two of the nine Bexar County invertebrates) was found in a borehole that encountered a void about 600 ft (183 m) from the nearest cave (Horizon 1991). Detectability data support that karst invertebrates occupy mesocaverns (connected to known caves) possibly more often than they occupy the caves themselves (Krejca and Weckerley 2007). For example, it is not uncommon to thoroughly survey a cave and find no karst invertebrates and then on the next survey, find many individuals. This is likely because the species were in mesocaverns during the previous survey (Krejca and Weckerley 2007). Ueno (1977) in Japan found that many troglobites live both in caves and in shallow mesocavernous habitats. Howarth (1983) found through survey data that the endangered Kauai Cave wolf spider (*Adelocosa anops*) and amphipod (*Spelaeorchestia koloana*) in Hawaii occupy mesocaverns adjacent to larger cave passages.

Mesocavern connectivity has been suggested by genetic research that showed gene flow between occupied caves separated by many miles (Paquin and Hedin 2004). Paquin and Hedin (2004, 2005) in Bexar and Travis counties, found *Cicurina* spiders with shared mtDNA haplotypes occurring in caves separated by distances of over several kilometers. In these instances, mtDNA from multiple specimens from multiple caves failed to sort in the resulting phylogenetic trees according to cave as would be expected if the caves contained discrete populations. In other words, spiders from different caves were in some cases more closely related than spiders collected from within the same cave. White (2006) studied the Bexar County example and found that Hilger Hole, Eagle's Nest, Root Canal, and several other unsampled caves within and adjacent to Camp Bullis likely functioned as a single habitat patch due to a common paleohydrologic origin and similar genetic relatedness. In other words, all of these caves formed within the damage zone of a fault, where interconnected mesocaverns and entranceless caves are likely to occur. In Travis County, Ledford (2011) found identical haplotypes of Tooth Cave spider (*Neoleptoneta myopica*), in four caves, the most distant of which are about 290 m apart. Ledford (2011) also found identical haplotypes in *Neoleptoneta sandersi*, an unlisted related species, from three caves in Travis County, the most distant of which are more than 2 mi apart. He also found identical haplotypes for *Neoleptoneta anopica*, another unlisted, related species, in two caves in Williamson County, Texas that are 1.9 miles apart (Ledford 2011).

Mesocavernous voids can be categorized on the basis of physical characteristics, particularly in regard to water movement. Mesocavernous voids less than 0.7 inch (in) (2 millimeter (mm)) wide act as capillaries and tend to hold water. Water tends to flow in voids that are between 0.2 to 0.4 in (5 to 10 mm) wide depending on flow conditions (G. Veni, National Cave and Karst Research Institute, pers. comm. 2008). These smaller voids are more likely to become plugged with sediment when they carry water. They also are able to hold only minimal amounts of food resources, such as dissolved organic matter (Howarth 1983, Holsinger 1988, Elliott and Reddell 1989). In voids that are 0.4 to 0.6 in (10 to15 mm) (depending on flow conditions), water flow becomes turbulent, meaning that it can carry more suspended particles, including organic debris. Voids tend to fill and wash open over time, with smaller voids filling more quickly and opening more slowly. Some mesocaverns may also be created by or filled by tree roots. While roots themselves are a documented source of energy, they may also provide pathways for water and nutrient travel (ZARA 2009)**,** or temporarily block pathways during growth then re-open them after the plant is dead and the roots decompose.

<u>2.2.3 Microhabitat</u>

Microhabitat (habitat within a cave such as under rocks), cave zones, and seasonality have been quantified for three of the karst invertebrates that occur on Camp Bullis, including

Rhadine exilis, *R. infernalis*, and *Cicurina madla* (Tables 2 and 3). These species were found in two or three of the three zones within the cave, including the entrance zone (near the cave entrance), the twilight zone (typified by limited light and more stable humidity and temperatures than the entrance zone), and the dark zone (typified by total darkness, stable humidity and temperature). *Rhadine exilis* were observed in 13 caves. The microhabitats (53 instances) occupied by *R. exilis* varied, with about 58 percent being found on the cave floor and 42 percent under rocks or on the undersides of rocks or other materials (Veni and Associates 2008). *Rhadine infernalis* were observed in three caves and were usually found under rocks (Veni and Associates 2008). *Cicurina madla* were observed in two caves and were always found among loose rocks or mud balls. In 52 of the 72 instances (72 surveys), they were found on the underside of rocks, the other times they were on top of rocks. Since they typically spin their webs underneath rocks and in crevices, they are probably dependent on this type of habitat (Veni and Associates 2008).

Table 2. Microhabitat occupancy as a proportion per total surveys

Species	Entrance Zone	Twilight Zone	Dark Zone
R. exilis	3/48	17/48	28/48
R. infernalis	6/23	10/23	7/23
C. madla	0	3/75	72/75

Table 3. Seasonality as a proportion per total surveys

Species	Fall	Spring	Summer
R. exilis	12/64	37/64	15/64
R. infernalis	1/23	13/23	9/23
C. madla	~25/75	~25/75	~25/75

<u>2.2.4 Drainage Basins</u>

Water primarily enters the karst ecosystem through surface and subsurface (groundwater) drainage basins but can also percolate through the soil and mesocaverns as demonstrated by several studies (Cowan et al. 2007, Hauwert 2009, Veni and Associates 2008). Well-developed pathways, such as cave openings, fractures, and solutionally enlarged bedding planes, rapidly transport water through the karst with little or no purification (White 1988). Therefore, caves and karst are susceptible to pollution from contaminated water entering the ground (Drew and Holtz 1999). The surface drainage basin is dependent on topography and slope. It typically includes the cave entrance, adjacent sinkholes, and the adjacent soil (Cowan et al. 2007, Hauwert 2009). The subsurface drainage basin includes mesocaverns, subterranean streams, bedding planes, buried joints, and sinkholes that have a connection to the surface that is not always observable from the surface (Veni and Associates 2002). It is also important to note that the surface and subsurface drainage basins do not necessarily overlap and may be different sizes and trend to opposite directions (Veni 2003). It is critical to have drainage basins with a natural quantity and quality of water because cave fauna require high humidity and material brought in from the surface (see discussion below).

2.2.5 Humidity and Temperature

Terrestrial troglobites require stable temperatures and constant, high humidity (Barr 1968, Mitchell 1971a). The temperatures in caves are typically the average annual temperature of the surface habitat and vary much less than the surface environment (Howarth 1983, Dunlap 1995). Relative humidity in a cave is typically near 100 percent for caves supporting troglobitic invertebrates (Elliott and Reddell 1989, TPWD 2010, SWCA 2010). Many of these species have lost the adaptations needed to prevent desiccation in drier habitat (Howarth 1983) or the ability to detect and/or cope with more extreme temperatures (Mitchell 1971a). To maintain these conditions, it is important to maintain an adequate drainage area that supplies moisture to caves and to maintain the surface plant communities that insulate karst ecosystems from excessive drying and extreme temperature fluctuations (Elliott 2000).

2.2.6 Nutrients

Nutrients in most karst ecosystems are derived from the surface (Barr 1968, Poulson and White 1969, Howarth 1983, Culver 1986) either from organic material washed in or brought in by animals or by feeding on the karst invertebrates that feed on surface-derived nutrients. Habitat changes that affect nutrient sources can affect listed karst invertebrates because they are at the top of their food chain (Culver et al. 2000). Primary sources of nutrient input include leaf litter, root masses, and trogloxenes (species that spend part of their life underground and part on the surface). An example of the karst food chain may be the following: a tree drops leaves, which decay and are eaten by small leaf litter invertebrates; cave crickets eat the surface invertebrates (and some of the fungi that grow on the leaves); the cave crickets defecate in the caves; the cave cricket feces are fed upon by collembolan, which are then captured by a predatory karst invertebrate such as *Cicurina* or *Tayshaneta* species. For predatory troglobites, accidental species of invertebrates (those that wander in or are trapped in a cave) may be an important nutrient source in addition to other troglobites and troglophiles (a species that may complete its life cycle underground but may also be found in dark, moist environments on the surface) found in the cave (Service 2000). Taylor et al. (2004) found that there is a close dependence of predators upon prey within the karst ecosystem. In some cases, the most important source of nutrients for a karst invertebrate may be the fungus, microbes, and/or smaller troglophiles and troglobites found on the leaves or feces left inside a cave (Elliott 1994, Gounot 1994). In deeper cave reaches, nutrients enter through water containing dissolved organic matter percolating vertically through karst fissures and solution features (Howarth 1983, Holsinger 1988, Elliott and Reddell 1989).

The cave cricket (*Ceuthophilus* spp.) is a particularly important nutrient component (Barr 1968, Reddell 1993) and is found in most caves in Texas (Reddell 1966). The energy input from foraging by tens to thousands of crickets is quite large, with deep cricket guano blanketing large parts of the floor of some cave passages. A variety of troglobites are known to feed on cave cricket guano (Barr 1968, Poulson et al. 1995), eggs (Mitchell 1971b), and/or on the adults and nymphs directly (Elliott 1994). Research conducted by Taylor et al. (2007a) found that the total number of cave taxa was strongly correlated with the total number of cave crickets (*C. secretus* and *C.* species B). This is an indicator of the importance of cave crickets to the karst ecosystem.

The trophic position (or place in the food web) and abundance of cave crickets was examined by Taylor et al. (2007a). The most abundant recognized species of cave cricket in central Texas is *Ceuthophilus secretus*. There is at least one other widely recognized, but not formally described, species of cave cricket referred to as "*Ceuthophilus* species B." Both of these species are opportunistic scavengers known to exit caves at night and forage on items including fungi, ripe persimmon fruit, and dead insects on the surface, therefore they are important pathways of nutrients into the cave (Taylor et. al 2007a). One study documented that cave crickets travel up to 105 m (345 ft) from the cave entrance (Taylor et al. 2005). Mark-recapture (Taylor et al. 2005) and radio-tracking data (Taylor et al. 2004) corroborate high cave cricket migration between sites. Typically, cave crickets exit a cave to forage when the ambient surface temperature is close to 15º Celsius (59º Fahrenheit) and the relative humidity is close to 100 percent (Lavoie et al. 2007). Cave crickets are generally known to return to the cave during the day, where they lay eggs and roost. A recent radio tracking study showed that travel from cave to cave is not uncommon; and sometimes the crickets will spend their day on the surface away from a known cave, probably in a tiny crack or other protected microhabitat (Taylor et al. 2004). A third species, *Ceuthophilus cunicularis*, is more troglomorphic and almost never found exiting the cave. The taxonomy of this group is not well studied, and the observed morphological variation indicates there may actually be many species that occur across the state (Taylor et al. 2007b).

A cave harvestman (*Leiobunum townsendi*) is another invertebrate trogloxene that is widespread and commonly found in Texas caves (Reddell 1965). Vertebrate species that have been frequently found in caves and may be important trogloxenes in some cave systems include raccoons (*Procyon lotor*), slimy salamanders (*Plethodon albagula*), cliff frogs (*Eleutherodactylus marnockii*), various species of mice (primarily *Peromyscus* spp.) and snakes (Reddell 1967).

In some instances, eutrophication (excessive nutrients) of the surrounding surface environment may attract trogloxenes, which often take shelter inside caves. This can result in the trogloxenes bringing excess nutrients into a cave. For example, observations of decreased troglobitic diversity have been made in some caves that have excessive raccoon scat (Balcones Canyonlands Preserve 2005, 2006, 2007).

2.2.7 Surface Vegetative Community

Surface plant communities are important components of karst ecosystems. They provide nutrients for trogloxene species on the surface and for karst invertebrates through leaf litter and roots that either wash or grow into caves (Howarth 1983, 1988, Jackson et al. 1999; also see our preserve design document at https://www.fws.gov/library/collections/terrestrial-karst-invertebrates [Service 2011]) for more information on the importance of vegetation in relation to preserve design]. Surface vegetation also acts as a buffer to edge effects and to the subsurface environment against drastic changes in the temperature and moisture regime. It also serves to filter pollutants (to a limited degree) before they enter the karst system (Biological Advisory Team 1990).

2.2.8 Surface Animal Community

Natural quantities of surface vertebrates and invertebrates are important components of a functioning ecosystem. Surface invertebrates that enter or are washed into caves provide food for trogloxenes, such as cave crickets, bats, toads, frogs, and for some karst invertebrates. Many of the vertebrate species that occasionally use caves bring in a significant amount of energy in the form of scat, nesting material, and carcasses. Also, healthy native arthropod community may better stave off red-imported fire ants (*Solenopsis invicta*) (RIFA), a threat to the karst ecosystem (Porter et al. 1988, 1991, Taylor et al. 2003).

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