FINAL PERFORMANCE REPORT

Federal Aid Grant No. F16AF01211 (T-96-R-1)

Distribution and Biology of the Oklahoma-endemic Wichita Mountains Pillsnail

Oklahoma Department of Wildlife Conservation

July 1, 2017 – December 31, 2020

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Project Leader/Principal Investigator: Elizabeth Bergey and Alexander Cooper, Oklahoma Biological Survey, University of Oklahoma

ABSTRACT

The Wichita Mountains pillsnail, *Euchemotrema wichitorum*, was originally described in 1972 from surveys in parts of two counties in southwest Oklahoma. Virtually all that was known about this species was in this one publication. The goal of this study was to investigate this snail's distributional range, habitat use, and aspects of its natural history so that we may better understand and conserve this restricted endemic species. We located *Euchemotrema* in 70 of 106 sites across 9 of the 15 counties surveyed. Sixty-five of those 70 sites were assigned to *E. wichitorum.* We estimate the species' range to be approximately 4700 km², which is significantly larger than the earlier two-county range. A General Additive Model of multiple microhabitat conditions explained 57.5% of the variation in live snail abundance and indicated that this species is strongly associated with factors correlated to increased forest density, particularly the availability of logs large enough to use as shelter sites. Interestingly, although fires that entirely burned shelter logs are highly detrimental and cause mass mortality, *E. wichitorum*'s abundance also had a positive association with less severe fires. Sites with fire evidence averaged about six times the number of live snails than sites without fire evidence and charred shelter logs had about double the abundance of logs without burn evidence. Analysis of soil pH from 34 survey sites showed that fire increased soil pH, which is typically associated with increased snail abundance. Increased abundance may occur after low-severity fires due to an influx of bioavailable calcium as calcium oxalate in the leaves and bark of the dominant tree species, Post Oak (*Quercus stellata*), is converted into soluble calcium ions and calcium carbonate. Genetic analysis comparing 40 individuals from various populations of *E. wichitorum*, *E. leai*, and questionable

Euchemotrema from western Oklahoma was able to distinguish populations confidently assigned to species level as well as help delimit some of the indistinct populations. Field and laboratory observations found snail breeding activity peaks at the onset of the growing season and that *E. wichitorum* egg clutches tend to have fewer eggs than those of *E. leai.* Overall, *E. wichitorum*'s long-term conservation prospects are good when considering that the species' range is much larger than previously known and individual populations persisted through all but the most severe fires. If ever needed, this species can be easily maintained and bred in captivity.

OBJECTIVES:

1) Determine the distribution of *Euchemotrema wichitorum* within Oklahoma, including on federal, state, and private lands.

2) Describe the microhabitat(s) used by the snail.

3) Investigate the effects of recent controlled burns and wild fires on the species.

4) Gather information about the biology and natural history of this species.

INTRODUCTION

Prior to our survey, the Wichita Mountains pillsnail (= 'pillsnail') (*Euchemotrema wichitorum*) was known only from the Wichita Mountains, where it was first described in 1972 by Branley Branson as occurring in two counties: Comanche and Caddo Counties (Hubricht 1985). NatureServe ranks the species as G2 and it had not been assigned a state rank because data on this species were deficient. It is a Tier I species in the Oklahoma Comprehensive Wildlife Conservation Strategy.

Beyond this original report, the species has since been found at least three times in the Wichita Mountains Wildlife Refuge (WMWR), where the species is not rare. This study surveyed of the snail's distribution both within and beyond the Refuge, as well as determining the microhabitat(s) used by the species. Fire is an often-used conservation tool that can strongly impact land snails (Gaines et al. 2011; Hylander 2011; Nekola 2002) and recovery can be slow (Beetle 1997). Effects of fire were assessed by surveying snails in burned (both controlled and wildfire areas) and nearby unburned areas.

This project provided much needed information about this little-known endemic snail in Oklahoma. Knowing more about the distribution, biology, and any impacts from fire provides the basis of a conservation plan and helps secure the species' future.

Description of the species. *Euchemotrema wichitorum* was described as *Stenotrema wichitorum* in 1972 (Branson 1972). After the original description, all known reports of this species in the literature are its inclusion in lists of species, based only on this one Branson publication (e.g., Hubricht 1985; Perez and Cordeiro 2008; Turgeon et al. 1998). *Euchemotrema wichitorum* is in the family Polygyridae, which are characterized by a recurved lip on the shell's aperture at maturity, making it easy to distinguish adults from immatures. Polygyrids typically occur in colonies and, in Oklahoma, typically occur in both the leaf litter-soil interface, and under logs and rocks. The shell of *E. wichitorum* is 7.5 to 9 mm in diameter and the aperture has a distinctive low, wide tooth extending form the body whorl that partly closes the shell aperture (Fig. 1, Branson 1972).

Biology. The biology and natural history of this species was unknown. In the species description, Branson states 'It is a species characterizing the semi-arid Wichita Mountains', which comprises the only hint of its ecological niche. In a 2013, 3-hr survey (Nekola and Bergey), the species was found at the base of rock outcrops, but this was also the targeted habitat, so it may not cover the extent of the snail's microhabitat range. That survey, however, demonstrated that the species was common enough to feasibly study.

Similar species. *Euchemotrema hubrichti*, like the Wichita Mountain pillsnail, has a small distribution - living in limestone outcrops in two counties in southwest Illinois (Anderson 2005). All known populations are on federally protected areas. In the conservation plan for the species (Anderson 2005), the greatest threat to *E. hubrichti* is considered to be fire – both in the form of controlled burns and wildfires. This proposed threat is based on effects of fire on other snail species (e.g., Hylander 2011; Nekola 2002), as fire effects have not been investigated in any *Euchemotrema* species.

Euchemotrema leai aliciae, is a widespread land snail throughout the eastern US (Hubricht 1985, Fig. 1) and is believed to be the most closely related species to *E. wichitorum* (Branson 1972). This species has a range that extends into central Oklahoma (Fig. 1) and closely resembles *E. wichitorum*, with the primary morphological differences being shell height and color. *E. wichitorum* has a relatively shorter shell at similar widths and tends to be lighter in color (Fig. 1).

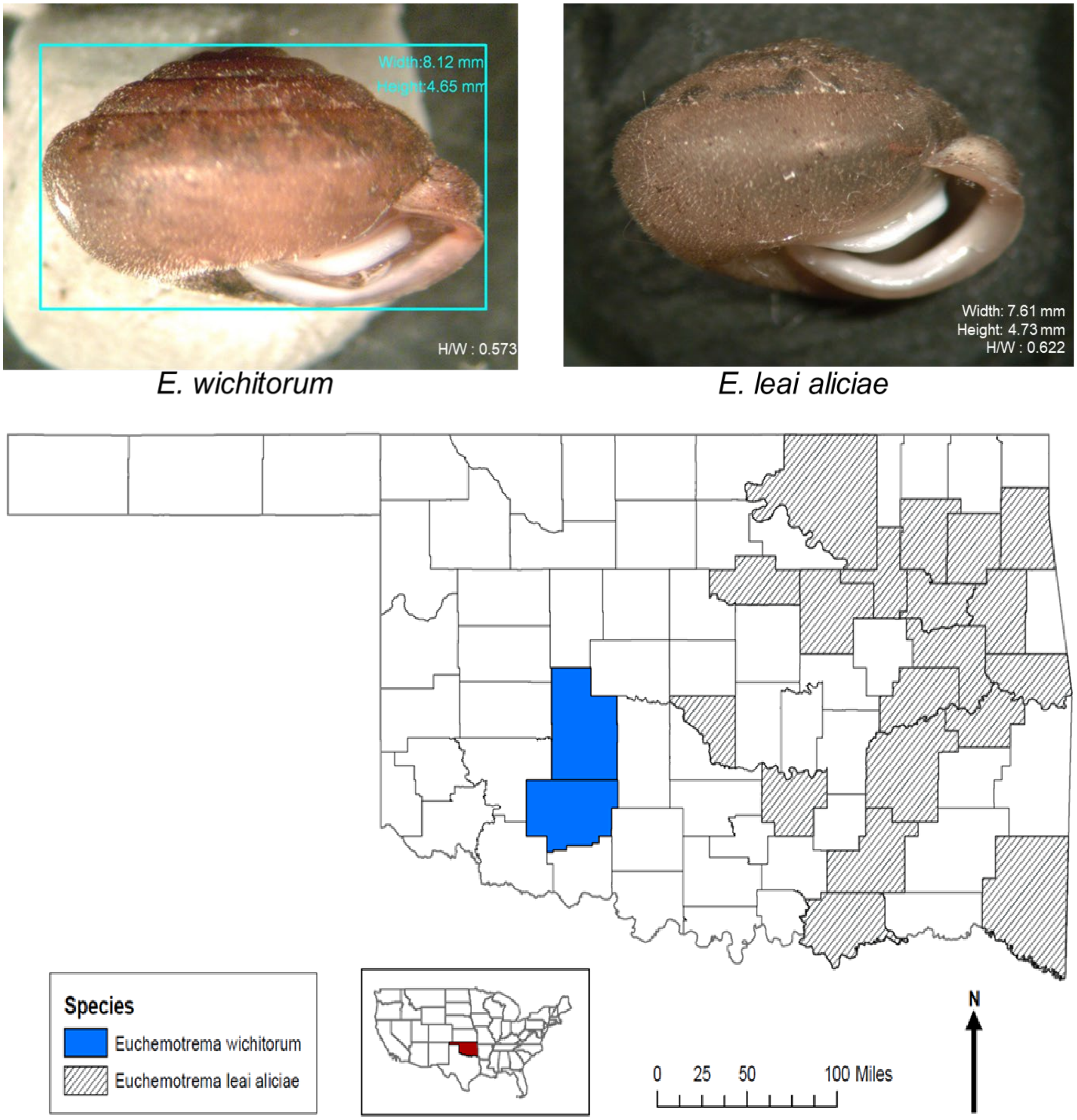

Figure 1. Pictures of the shell and ranges *E. wichitorum* and *E. leai aliciae*. The shell of *E. wichitorum* tends to be relatively shorter (small Height/Width ratio) and has a lighter color than *E. leai.* Photos (by Alex Cooper) are shown at the same scale The map shows the previously known distribution of *E. wichitorum* and *E. leai* based on the museum collection records of the Field Museum of Natural History, the Carnegie Museum of Natural History, and the University of Florida Museum of Natural History.

APPROACH

Core Strategy

This project was centered around field surveys for snails and components of all objectives were accomplished through these surveys. The survey approach used timed visual surveys to confirm snail presence and to quantify abundance at each surveyed location, which was augmented by collection of environmental data.

Snails commonly occur at the junction of leaf litter and soil, so visual searches generally entail sweeping aside small areas (< 1ft^2) of leaf litter at a time and looking for snails and then returning leaf litter. Other areas checked include the undersides of logs and non-embedded rocks. Surveys were generally for 30 minutes of search time.

The initial strategy was to assess where the snail occurred within the Wichita Mountains Wildlife Refuge (WMWR) and then to expand to other areas after gaining insights into where live snails tended to be found. We sampled all habitat types in the WMWR with sufficient shelter habitat for snails, including post oak-blackjack woodlands of varying density, boulder-dominated hillsides, riparian woodlands, stands of sugar maple, and red cedar woodlands.

Range

Numerous surveys within the WMWR revealed that live snails are most likely to be found under logs in dense woodlands, particularly Post Oak, Sugar Maple, and riparian stands. After coming to this understanding, we expanded our survey efforts to wooded areas across much of western Oklahoma. Potential sites were primarily identified via satellite imagery (Google Maps) and were surveyed once permission from landowners or managers was obtained.

The specific search site was selected within our target region based on the presence of logs or boulders to serve as shelter habitat for snails. Because the surveys conducted outside of the WMWR had the additional goal of establishing *E. wichitorum* presence in locations outside the previously known range of the species, these areas were searched until either all potential shelters in an area were examined or approximately 60 minutes of search time produced no shells or live *Euchemotrema* snails. No locations surveyed beyond the standardized 30-minute timeframe had *Euchemotrema*.

We estimated the range of *E. wichitorum* in ArcGIS through construction of a minimum convex polygon (Hayne 1949) that encompassed all survey points containing *Euchemotrema* populations that could be confidently assigned to *E. wichitorum* based on a combination of shell morphology closely matching the species description and individuals from the WMWR and genetic screening. Five *Euchemotrema* populations in western Oklahoma could not be confidently assigned to *E. wichitorum* and were excluded from the range estimate (Fig. 2). A 3 km buffer was used around each boundary-defining site. An area of largely unsuitable habitat (flat agricultural land and a developed portion of the city of Lawton, OK, lacking any large tree stands) was excised from the southern portion of the range polygon to produce a more conservative and accurate estimate of range area (Grueter et al. 2008).

Microhabitat and Fire

Data Collection**.** A variety of habitat variables were measured at field survey sites with *Euchemotrema* to determine environmental factors associated with snail abundance. These data were recorded at all survey sites within the WMWR and all range-expansion survey sites where *Euchemotrema* were located.

The following data were recorded at each site: GPS coordinates, fire evidence, general dominant vegetation (tree species, grass, forbs), and general habitat type in relation to tree and boulder density, and a site photograph was taken. Fire evidence at survey sites was recorded only as presence/absence because site-specific fire history was typically unknown.

Starting with field surveys in 2018, we further described the area around the shelter of highest snail abundance within the site by making it the center of a 12 m x 12 m plot where additional environmental data were recorded. We counted the number of shelter logs (defined as any log with diameter >5cm with at least 15cm of flush soil contact), boulders, and estimated litter cover, counted the number of trees taller than 2 meters and estimated canopy cover across the plot. Canopy cover was measured with a spherical crown densiometer (Forestry Suppliers) at five points taken within the plot and averaged. For surveys within the WMWR with shells but no live snails, a random (potential) shelter site was chosen as the center of the 12 m x 12 m plot. All but two of the 48 WMWR field survey sites from 2017 were revisited between 04/08/2018 and 07/09/2018 for collection of plot data, with one site being revisited on 01/31/2019. A portion of the sites were affected by an April 9, 2018 controlled burn. The fire severity was not high enough at any sites to combust logs or down standing trees but did affect the litter layer of several sites. In those cases, we used site photographs taken during the initial survey as a reference to help estimate litter coverage at time of initial survey.

For all new field surveys conducted in 2018 and 2019 (Table 1), we recorded additional data for each shelter log where we located snails to see if differences in shelter habitat conditions were associated with differences in abundance. We recorded the snail species, number of live individuals, and number of shells for each shelter log. We recorded the adjacent litter type (grass/leaves/cedar needles/mixed), measured the shelter size (length, circumference, and relative size) to see if larger shelters, which should theoretically provide larger and more thermally insulated habitats, had more snails. We also measured shelter-adjacent litter depth as an average of three points (either end and the approximate center) to see if a thicker litter layer, which provides more thermal insulation and potential food, had more snails. We also directly tested the relative thermal insulation of shelters by measuring the difference in temperature between soil directly underneath a shelter and the adjacent exposed surface litter temperature to see if shelters providing greater thermal protection had more snails. We measured temperatures with a Fluke 62 Max+ Infrared Thermometer. Relative soil moisture (dry to the touch, some moisture, or soil saturated) was measured to see whether moist shelters, which should lessen desiccation stress, had more snails than drier shelters. Lastly, we recorded burn evidence (charring of shelter or adjacent litter) at each shelter.

We collected soil samples for pH measurement from 33 of the 2017 field survey sites while they were being revisited during 2018. We also collected soil from one 2018 survey site. We took soil samples from beneath shelter sites (logs and boulders) and one meter away to test if shelter site pH differed from local soil pH (Müller 2005).

We took several approaches to assess the impact of fire on snail populations. We recorded burn evidence at all survey sites based on presence of obvious burn patches, ash around logs and boulders, and charred logs and trees. We compared the abundance of snails under shelters with and without burn evidence from burned and unburned sites, meaning a portion of the logs without burn evidence came from burned sites. We also measured soil pH from sites with and without burn evidence. Several of the revisited sites had burned since the initial visit and, consequently, burn evidence for soil pH data was based on site conditions at the time of soil sampling rather than on the conditions during the original visit. Lastly, we surveyed several areas

(2018-1, 2019-14, several 2017 sites remeasured in 2018; Table 1) burned recently enough that the site was still covered in ash and the primary successional vegetation had not yet established, to observe whether there were signs of mass mortality (bleached shells in ash outlines of logs, in ash piles surrounding boulders, or scattered haphazardly in the open). Most burned sites appeared to be subject to low-severity fires, but several appeared to experience high-severity burns and one site (2019-14, Table 1) was surveyed three days after high-severity fire that burned all ground cover, completely combusted most logs, and downed many live trees, with some still smoldering at the time of survey.

Data Analysis. We used two separate General Additive Models (GAM) (Hastie and Tibshirani 1987) to model the live-snail abundance of *E. wichitorum* in relation to the measured habitat characteristics. The first GAM compared the live-snail abundance of *E. wichitorum* at 60 survey sites in relation to the site microhabitat characteristics measured in the 12 m x 12 m plots (Table 1). The second GAM compared live snail abundance to the measured characteristics of each shelter log containing snails, which were measured for 52 shelter logs from 14 sites surveyed in 2018 and 2019 (Table 1). We used counts of live snails in favor of a combination of live snails and shells because we were interested in suitable habitat and shells may can indicate both suitable and unsuitable habitat (where snails died).

The relationship between live snail abundance and the measured habitat characteristics in each 12 m x 12 m plot was compared with a General Additive Model (Hastie and Tibshirani 1987). Fire was modeled as a fixed effect because fire evidence at survey sites was recorded as a binary presence/absence, which prevented fire from being modeled as a smooth function. The GAM was checked for problematic variables using the MGCV function gam.check. This GAM included data from 60 field survey sites (Table 1). For survey sites outside the WMWR, we included those with snails that could be assigned confidently to *E. wichitorum* or populations that had at least one sampled individual sort with the main clade *E. wichitorum* individuals during preliminary genetic screening (Fig. 7, Table 2). A few sites (2019-4, 2019-6, 2019-8, and 2019-13; Table 1) were riparian forests with large quantities of driftwood logs, often in large piles. Two of these sites, 2019-6 and 2019-8, had large driftwood piles in the 12 m x 12 m plot. These sites were assigned them log values of 100 (an underestimate) to keep these unique *E. wichitorum* habitats in the model while mitigating their negative impact as outliers.

To further investigate the significant effect of fire indicated by the microhabitat GAM, we compared the number of live snails found at burned and unburned sites using a Bayesian analog of the t-test. We constructed a Bayesian model to test for a true difference, *D*, between the average number of live snails found at sites with and without burn evidence.

Shelter Analysis. We used the same analytical approach for analyzing the live snail abundance in relation to measured shelter log characteristics as was used between live snails and 12 m x 12 m survey site characteristics: We constructed a GAM of measured characteristics and, upon seeing fire (charring) had a significant effect, constructed a Bayesian analog of a t-test comparing the abundance of live snails associated with burned and unburned logs. The GAM and the Bayesian models for the shelter sites had the same underlying parameters (smoothing terms, distributional assumptions) as the survey site analyses described in the previous section and the outputs of the two Bayesian models are presented together for ease of comparison.

We analyzed 52 logs that harbored snails or shells from 14 field survey sites surveyed in 2018 and 2019 (Table 1). We used the same site selection parameters for this GAM as for the microhabitat GAM. Of the measured log characteristics, we modeled adjacent litter depth, log size characteristics (length, circumference, and volume), soil moisture (as a fixed effect), and fire evidence.

Soil Analysis. We measured the soil pH from 34 survey sites in the WMWR (Table 1). The data failed to meet the assumption of normality. The non-normal dataset was then analyzed using a Bayesian analog of a two-way ANOVA with shelter soil vs. open soil (taken 1 meter away from the shelter), site burn evidence, and their interaction as the three factor levels.

Biology and Natural History

Breeding phenology. We investigated breeding phenology and behavior of *E. wichitorum* to better understand its conservation needs. Eggs and young snails are particularly sensitive to desiccation (Asami 1993), meaning the potential negative impact of fire on *E. wichitorum* populations is magnified if it occurs while eggs are incubating or before juveniles spread from their incubation shelter. We used a combination of field surveys, laboratory observation, and breeding trials to determine breeding timing, oviposition behavior, fecundity, and density requirements.

Field surveys were conducted throughout the year and all observations of eggs and juveniles were noted. Several laboratory colonies were started from wild populations, typically with five founders per population. Colonies were supplied with ample leaf litter for food and shelter, with regular supplementation of water, romaine lettuce, and various vegetables (sweet potato, carrot, cucumber). Colonies were regularly checked for eggs and young, with colony censuses done when changing habitat containers. An initial set of colonies was more closely documented during the first several months of 2018, with all egg clutches counted and their deposition depth measured. We also attempted breeding trials between *E. wichitorum*, *E. leai*, and *S. labrosum* by quarantining individual snails for several months and then combining pairs and documenting egg clutches for several additional months.

Genetics. We analyzed the DNA of 40 individuals from populations *Euchemotrema wichitorum*, *E. leai*, and undetermined populations in western Oklahoma (labeled *E.* westOK) to investigate the genetic distinctness of *E. wichitorum* and to help delimit populations that were morphologically intermediate between the two species. We compared these individuals using the mitochondrial gene COI and a nuclear barcode gene of the large ribosomal subunit (Wade et al 2004).

All sampled individuals were collected, drowned, and had DNA extracted, amplified, and purified by AC Cooper. Samples were sequenced using BigDye reactions on ABI 3130xl Genetic Analyzer in the Biology Core Molecular Lab by technician Ann Stafford. Sequence alignments and Bayesian phylogenetic tree construction were done using Geneious Prime ver. 2021.0.3 software using the MAFFT and MrBayes plugins, respectively. The Bayesian tree was constructed using both genes simultaneously and thus it only includes individuals successfully sequenced for both genes. The individuals presented here covered most of the sampled populations in Oklahoma, but we plan to do additional analyses incorporating individuals with single-locus coverage and individuals from other related species outside of Oklahoma into a publication in peer-reviewed journal. This future publication will represent a follow-up to this report and results of this larger study will be useful for assessing the genetic diversity of *E. wichitorum* compared to related species and further exploring its evolutionary relationship to *E. leai*.

RESULTS AND DISCUSSION

Range

Euchemotrema were found at 70 of the 106 survey sites and in nine of the 15 surveyed counties (Fig. 2). Some populations outside the WMWR were of intermediate shell morphology between *E. wichitorum* and *E. leai* and could not be confidently assigned to *E. wichitorum* and thus were excluded from the estimation of range (Fig. 2, 2019-2, 2019-3, 2019-8, 2019-12, 2020-3, Table 1). The estimated range of *E. wichitorum* covers an area of 4722 km^2 and extends beyond the WMWR into Caddo, Comanche, Cotton, Jackson, Kiowa, Stephens, and Tillman Counties (Fig. 3). *Euchemotrema wichitorum* was not found in the western, isolated portion of the Wichita Mountains around the southern portion of Lake Altus (mostly within Quartz Mountain State Park) and around the town of Granite, OK. However, *E. wichitorum* was found throughout the extent of the core portion of the Wichita Mountains, Mt. Scott in the eastern portion of the WMWR to the western extent of the main formation which runs northeast to southwest starting at the Blue Mountains northwest of Cooperton, through the Glen Mountains north of Tom Steed reservoir, and ending at the Navajo Mountains east of Friendship. The population found in the Navajo Mountains now represents the known western extent of the species. Populations were found south of the Wichita Mountains along both Cache Creeks, which drain most of the Wichita Mountains formation. Interestingly, a population of snails was also found just north of Waurika Lake on a floodplain of Beaver Creek that does not drain the Wichita Mountains, but instead an area east of the Wichita Mountains that is predominantly flat agricultural land. These three floodplain populations were found in streamside forests that receive deposits of driftwood during flooding events and now represent the known southern extent of the species. Populations of *E. wichitorum* were also found along forested ridges southwest of Anadarko, and in a drainage southwest of Carnegie, which now respectively represent the known eastern and northern extent of the species.

The range of *E. wichitorum* is much larger than initially expected based on its original description of two counties (Branson 1972; Hubricht 1985; Fig. 1). *Euchemotrema wichitorum*'s range includes several woodland areas well outside the Wichita Mountains formation, suggesting that its ties to the Wichita Mountains stems from this area providing large islands of woodland habitat in a sea of mixed-grass prairie and agricultural land rather than an association with the unique granitic geology typical of the region. The association with wooded areas is consistent with its close relation to the forest-dwelling *E. leai*, rather than an association with unique rocky habitats exhibited by two other related species, *E. hubrichti* and *Stenotrema pilsbryi*, whose endemism to regions of unique geology are because of a close habitat association with said geology (Anderson and Smith 2005; Mather 1998).

The presence of populations in drift deposition areas within riparian forests along streams that drain the Wichita Mountains indicates that *E. wichitorum* may be passively dispersed along waterways, as has been a suggested dispersal mechanism for other land snail species, based on population genetics data (Sinclair-Winters 2014; Liang et al. 2019). Riparian forests can support high abundances of land snails because the microclimate of these forests may be more mesic than other local habitats and these woodlands have an increased frequency of woody debris deposited by floods (Kappes et al. 2014).

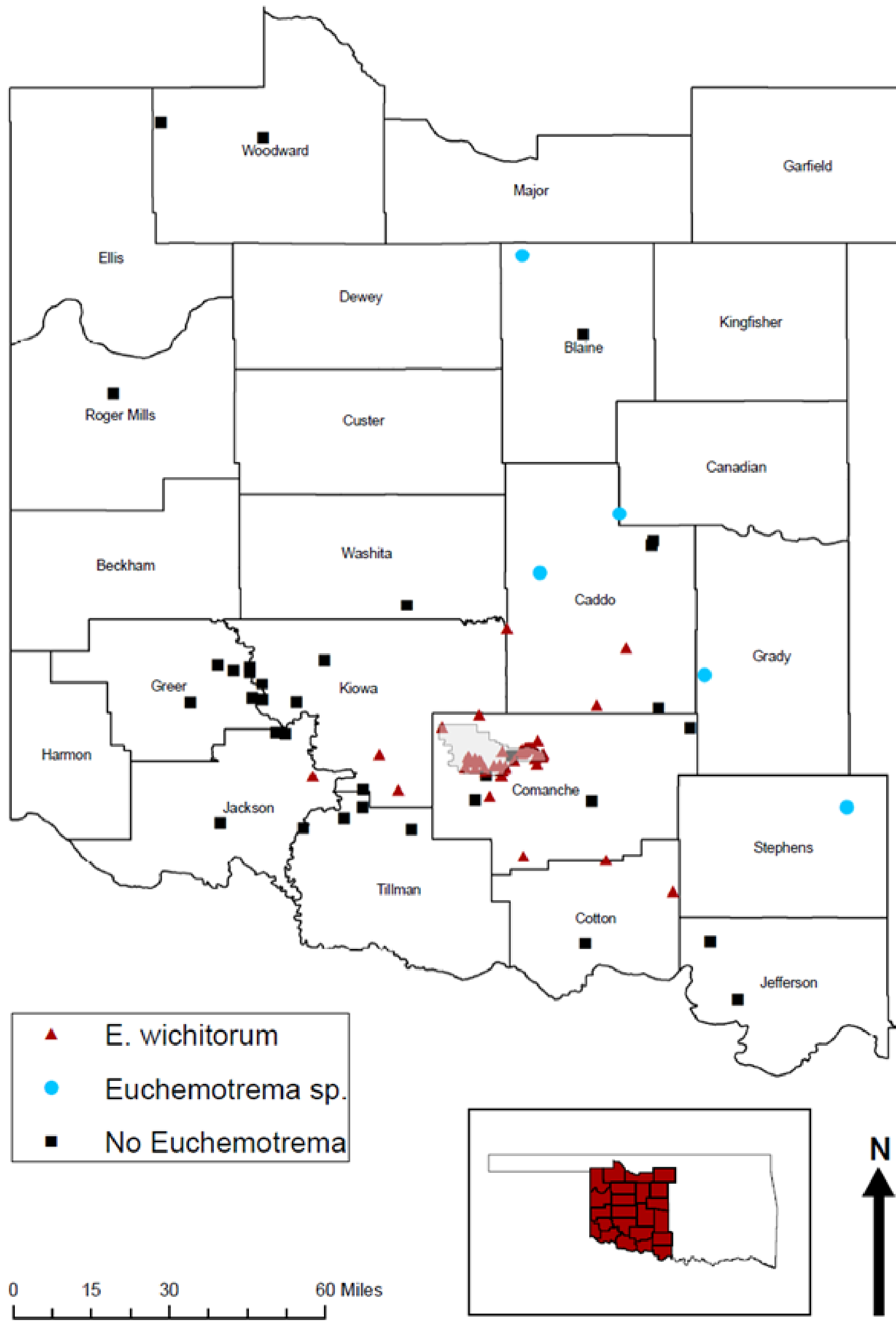

Figure 2. A map of the 106 western Oklahoma survey sites. Red triangles are populations that could confidently be assigned to *Euchemotrema wichitorum* (n = 65). Five populations of *Euchemotrema* could not be assigned to *E. wichitorum* (blue circles). Sites where no *Euchemotrema* were located are represented by black squares (n = 36).

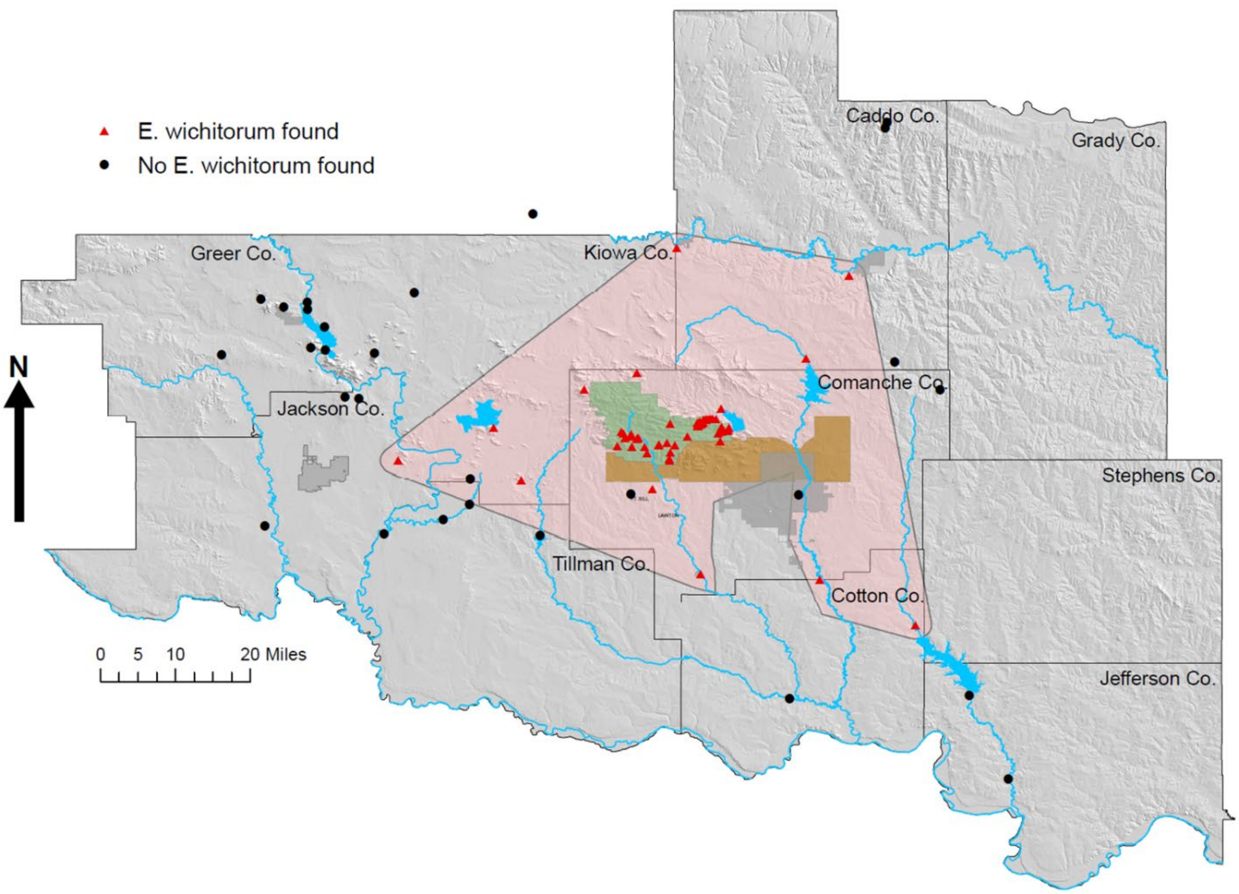

Figure 3. Map showing the estimated range of *E. wichitorum* based on our surveys (pink polygon). Red triangles indicate areas where *E. wichitorum* was found, while black circles indicate surveys that did not locate and *Euchemotrema* shells. The range covers an estimated 4,722 km^2 across seven counties and is significantly larger than the original description to northern Comanche and southern Caddo Counties. Additional sites were surveyed outside of the pictured area, but definitive *E. wichitorum* were not located.

Microhabitat

The general additive model (GAM) of the microhabitat conditions measured in the 12 m x 12 m plots explained 57.50% of the variance of live snail abundance. The count of shelter logs and the count of boulders were statistically significant. The number of logs had a positive relationship with snail abundance (Fig. 4). The downward projection in the model at the higher log values represents a trend towards a lesser increase in snail abundance at very high levels of logs at two riparian driftwood sites, which are outliers in having many more available shelter logs. The number of boulders at the field survey sites had a negative relationship with snail abundance (Fig. 4). The number of trees and percent of leaf litter cover were positive but had non-statistically significant trends with increasing snail abundance (Fig. 4). Canopy cover was not associated with live snail abundance. Fire evidence was present at 13 of the 60 sites and had a significant, positive effect on live snail abundance when modeled as a fixed effect.

The GAM for shelter log characteristics and live snail abundance did not have any significant variables. As fixed effects, fire ($p = 0.026$) and soil moisture ($p = 0.013$) had significant, positive effects on live snail abundance. Overall, variance capture of the model was 31.4%.

Live snail abundance was significantly associated with increasing numbers of logs and decreasing numbers of boulders. In general, logs serve as key habitat for many snail species by providing moist, cool sites that shelter snails during harsh conditions and provide an incubation habitat for their eggs (Kappes 2005). Logs and boulders roughly define the gradient of habitat types in the Wichita Mountains that harbor *E. wichitorum*; with high numbers of boulders being characteristic of more open habitat that tends to be dominated by grasses and higher number of logs being characteristic of increasingly dense woodlands. More open habitat is generally characterized by few live snails, but many shells, while forest habitats generally had far more live snails than shells. This trend is likely because of low numbers of hard-to-detect snails living in open habitats, where shells may degrade more slowly, compared to denser populations of snails in forests, where shell breakdown is likely more rapid because of both increased moisture and increased consumption by living snails and other animals (Pearce 2008; Cadée 1999).

The positive, but non-significant association between snail abundance and density of trees and litter cover is also consistent with higher numbers of snails in forested areas. *E. wichitorum*'s association with forested habitat is not a surprise: forested areas have lower light conditions, cooler soil surface temperatures, higher relative humidity, and much more decaying organic matter than neighboring prairie (Karlin 1961). These microhabitat conditions are associated with increased food and reduced desiccation risk for snails, which can be drivers of land snail presence and abundance (Albuquerque et al. 2008; Čejka et al. 2008).

We found no evidence of boulders being appropriate habitat for *E. wichitorum*, as no shells or snails were found under the few boulders small enough to easily turn over. Additionally, little evidence of burrowing into soil has been observed in forested habitats or laboratory colonies (Alex Cooper, personal observation).

Fire

Burned survey sites had more than six times the number of live snails (mean ± SE of 7.23 ± 2.09 live individuals found during 30-minute survey) than sites with no burn evidence (1.17 ± 0.30). Among shelter logs where snails were found, charred logs had more than double the number of live snails (2.78 ± .038 live snails per log) than unburned logs (1.31 ± 0.25). Our Bayesian estimates of these values were significantly different, with no overlap in the 95% credible intervals for either estimate (Fig. 5). Soil from burned sites had significantly higher pH than soil from unburnt sites (7.69 ± 0.14 versus 6.90 ± 0.16, $p = 0.02$). The pH of soil under logs and one m away were not significantly different ($p = 0.24$).

Several sites in the WMWR were surveyed close enough to the burn date that ash still covered portions of the sites and vegetation had yet to recover. No surviving snails were found from burns that removed all vegetation from an area. Shells of *E. wichitorum* persist through even severe fire, as evidenced by shells documented in the white ash piles of completely burned logs. Because the white shells on the ground are so apparent in burned areas, burned areas lacking shells likely lacked snails before the fire.

Survey site 2018-1 (Table 1), which had been previously surveyed and contained known locations of logs harboring snails, was revisited after a low-severity controlled burn to determine the fate of snails. Although many snails survived, even where large portions of their shelter log burned, others likely died because the adjacent leaf litter caught fire and burned the area at the soil-log interface while leaving the rest of the log intact.

After fires, *E. wichitorum* shells were not observed in open prairie habitat, even when adjacent areas with shelters had over one hundred exposed shells. Slopes with forbs, but lacking other shelters sometimes had *E. wichitorum* shells.

The relatively higher number of snails in sites with burn evidence and under charred logs was an unexpected finding of this study. Fire has typically been shown to have a negative effect (Nekola 2002; Ross et al. 2019; Nicolai et al. 2020) or, at best, a neutral effect (Kiss and Magnin 2004; Gaines et al. 2011) on snail community diversity and richness. Certain fire-adapted species may have positive associations with fire insofar as it maintains a more open woodland habitat where they are competitive (Santos et al. 2012).

Surveying areas after fires showed that snails persist as long as the immediate portion of log they are under does not burn or, for snails at the edges of logs, leaf litter at the log-soil interface does not burn. However, the presence of numerous exposed shells in recently burned areas suggests that snails sheltering in litter, or whose log shelters burn, do not survive. Low-severity burns left mosaics that had no observed mortality of snails in unburned patches, while mortality in burned patches was largely dependent on shelter log combustion. High-severity fire that completely burned all woodfall and left little litter did not have any apparent live snails, instead, whitened shells were often visible within the ash outlines of logs. If snails are found in these areas within the next several years, it may indicate that some *E. wichitorum* survive high-severity fires through sheltering in cryptic refuges, as has been proposed for several species native to fire-prone areas (Kiss and Magnin 2006; Santos et al. 2009).

The negative effects of fire, beyond direct mortality, are explained by environmental alterations that increase desiccation risk: fire reduces litter and coarse woody debris, opens canopy, and makes the microclimate more xeric (Kiss and Magnin 2004). However, fire can also change the environment in ways that benefit certain snail species. Fire is generally associated with a temporary increase in soil pH and extractable calcium (Certini 2005), which are both typically associated with increased snail abundance (Martin and Sommer 2004). Soil pH measurements from sites in the WMWR showed burn sites had higher pH. In the WMWR the increased pH is likely to be partially the result of higher levels of calcium carbonate in oak ash (Misra et al. 1993). Indeed, ash from Post Oak (*Quercus stellata*) collected from the WMWR that was experimentally burned at approximately 500 – 550°C had a pH of 10.5 (Cooper unpublished).

Snails from environments with non-calcareous soil are dependent on vegetation for the calcium needed to produce their shells and make their eggs (Sulikowska-Drozd and Horsak 2007). Considering the non-calcareous granite and gabbro bedrock, a major source of calcium for snails in the woodlands of the WMWR is the leaf litter and decaying wood of the dominant tree, Post Oak. Post Oaks store a significant amount of calcium in their bark, in concentrations up to six times that of the average deciduous tree (Johnson and Risser 1974). However, oaks sequester calcium in their leaves, bark, and wood as calcium oxalate (Trockenbrodt 1994), which is a largely insoluble calcium salt that does not significantly increase soil pH in oak woodlands (Wäreborn 1969). Calcium oxalate can be difficult for animals to absorb (Weaver et al. 1987; Harbers et al. 1980) and is less favorable to snail growth and reproductive success than more soluble forms (Wäreborn 1979). Fire converts the calcium oxalate in oak and other wood into soluble calcium ions and then into calcium carbonate (Pereira et al. 2012), meaning that charred logs and leaf litter would be a better calcium source than their unburned equivalents. Other nutritive elements (K, Na, Mg, Si, S) are also converted to more soluble and mineralized forms by fire, which makes them more extractable from charred wood than from unburned wood (Ubeda et al. 2009; Pereira et al. 2011). Indeed, burned logs are associated with higher rates of snail growth and higher soil pH (Ray and Bergey 2015). The increased concentration of bioavailable calcium, other minerals, and higher pH caused by the charring of logs and litter by low-severity fires may be a reason burned survey sites and charred logs harbored more snails than their unburned counterparts, although it is possible some unconsidered factor drives these associations.

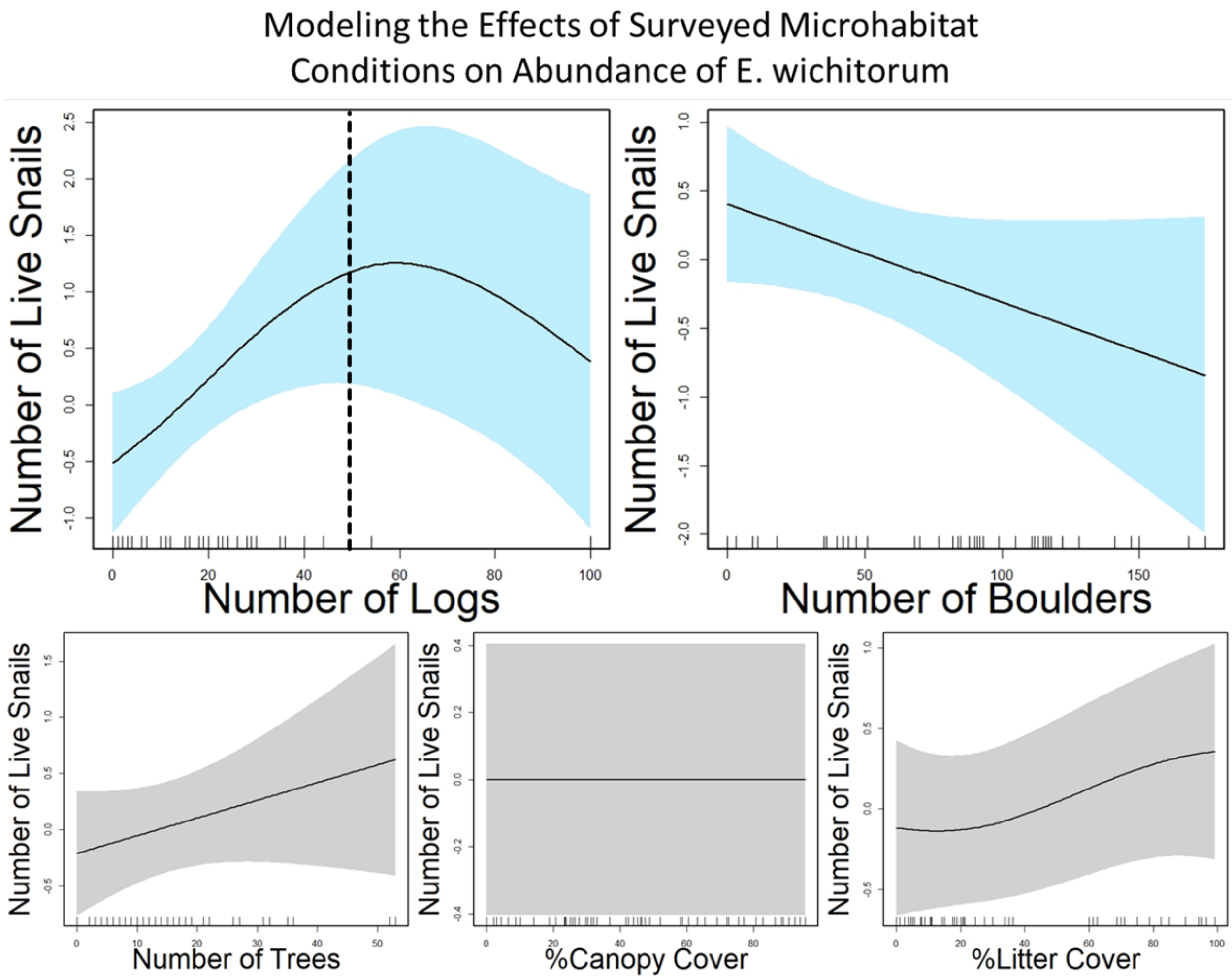

Figure 4. The response of live snail abundance to microhabitat conditions recorded in the 12 m x 12 m plot surveys as analyzed via our General Additive Model (GAM). Only the counts of shelter logs (p=0.011) and boulders (p=0.044) were statistically significant in the model. Shaded areas represent ±1 standard error around parameter estimate, with additional uncertainty in the confidence intervals around mean values depicted using seWithMean=TRUE (Marra and Wood 2012). The dashed line in the Number of Logs plot represents a break between riparian driftwood sites, which were the only sites with above 50 logs in a survey plot, and the rest of our survey sites, which were mostly Post Oak habitats that typically have fewer than 30 logs.

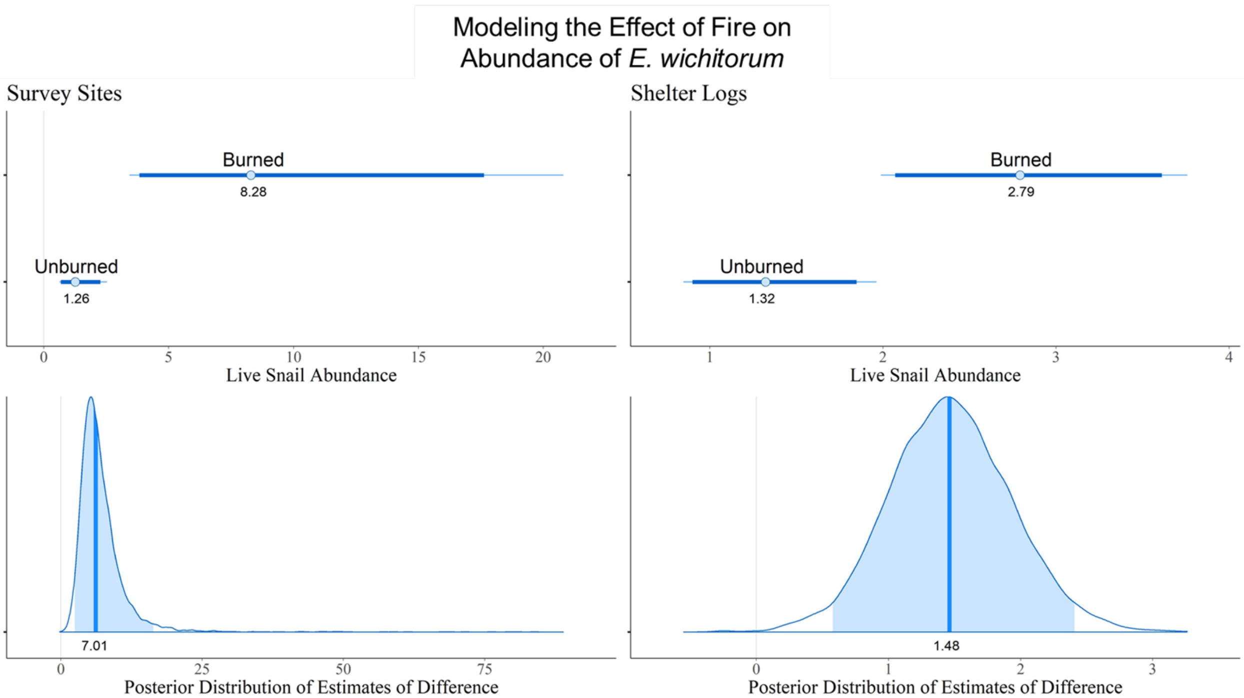

Figure 5. Bayesian modeling of the difference in number of live snails observed at survey sites with and without burn evidence (left) and under burned (charred) vs unburned logs (right). Numbers represent Bayesian mean estimates. 95% credible interval estimates are represented by the dark bars in the upper graphs and by the shading in the lower graphs. A lack of overlap in the intervals in the top graphs and the shaded region in the bottom graphs not containing zero both indicate statistical significance.

Table 1. All survey sites from this study. "Species ID" notes populations classification and was used for range-estimation purposes, which incorporated morphometric and genetic data; N/A = no *Euchemotrema* spp. found. "12 x 12: Yes" and "Log: Yes" notes sites used in the microhabitat and shelter GAMs, respectively. "pH: Yes" notes sites that had soil pH measurements. "DFA: Yes" notes populations included in a Discriminant Function Analysis (Cooper unpublished). "DNA: Yes" notes populations with individuals that have extracted DNA samples.

Species ID	Site Code	LAT	LON	County	Year	12 x 12	Log	Soil pH	DFA	DNA
E. wichitorum	2017-1	34.74401	-98.53265	Comanche	2017	Yes	No	Yes	Yes	No
E. wichitorum	2017-2	34.73722	-98.53396	Comanche	2017	Yes	No	Yes	No	No
E. wichitorum	2017-3	34.70544	-98.62356	Comanche	2017	No	No	Yes	Yes	No
E. wichitorum	2017-4	34.74712	-98.57836	Comanche	2017	Yes	No	Yes	No	No
E. wichitorum	2017-5	34.74828	-98.57841	Comanche	2017	Yes	No	Yes	No	No
E. wichitorum	2017-6	34.74828	-98.57821	Comanche	2017	Yes	No	Yes	No	No
E. wichitorum	2017-7	34.7373	-98.53226	Comanche	2017	No	No	No	No	No
E. wichitorum	2017-8	34.71816	-98.53466	Comanche	2017	Yes	No	No	No	No
E. wichitorum	2017-9	34.73808	-98.52763	Comanche	2017	Yes	No	Yes	No	No
E. wichitorum	2017-10	34.74773	-98.57881	Comanche	2017	Yes	No	Yes	No	No
E. wichitorum	2017-11	34.74992	-98.57645	Comanche	2017	Yes	No	No	Yes	No
E. wichitorum	2017-12	34.75625	-98.57448	Comanche	2017	Yes	No	Yes	No	No
E. wichitorum	2017-13	34.74606	-98.53263	Comanche	2017	Yes	No	Yes	Yes	No
E. wichitorum	2017-14	34.7808	-98.53326	Comanche	2017	Yes	No	Yes	No	No
E. wichitorum	2017-15	34.75034	-98.57269	Comanche	2017	Yes	No	Yes	No	No
E. wichitorum	2017-16	34.75205	-98.57169	Comanche	2017	Yes	No	Yes	Yes	No
E. wichitorum	2017-17	34.75361	-98.56915	Comanche	2017	Yes	No	Yes	No	No
E. wichitorum	2017-18	34.75436	-98.56805	Comanche	2017	Yes	No	Yes	Yes	No
E. wichitorum	2017-19	34.76082	-98.55728	Comanche	2017	Yes	No	Yes	Yes	No
E. wichitorum	2017-20	34.76079	-98.56173	Comanche	2017	Yes	No	No	No	No
E. wichitorum	2017-21	34.75935	-98.56631	Comanche	2017	Yes	No	Yes	Yes	No
E. wichitorum	2017-22	34.75276	-98.57913	Comanche	2017	No	No	Yes	No	No
E. wichitorum	2017-23	34.75932	-98.56774	Comanche	2017	Yes	No	Yes	No	No
E. wichitorum	2017-24	34.75909	-98.56248	Comanche	2017	Yes	No	Yes	No	No
E. wichitorum	2017-25	34.76049	-98.55415	Comanche	2017	No	No	Yes	Yes	No
E. wichitorum	2017-26	34.76025	-98.55173	Comanche	2017	Yes	No	Yes	No	No
E. wichitorum	2017-27	34.76017	-98.54273	Comanche	2017	Yes	No	Yes	No	No
E. wichitorum	2017-28	34.76071	-98.54942	Comanche	2017	Yes	No	Yes	Yes	No
E. wichitorum	2017-29	34.71231	-98.65341	Comanche	2017	Yes	No	Yes	No	No
E. wichitorum	2017-30	34.71141	-98.65427	Comanche	2017	Yes	No	No	Yes	No
E. wichitorum	2017-31	34.72736	-98.70704	Comanche	2017	Yes	No	No	No	No
E. wichitorum	2017-32	34.72419	-98.69275	Comanche	2017	Yes	No	Yes	Yes	No
E. wichitorum	2017-33	34.72503	-98.69545	Comanche	2017	Yes	No	Yes	No	No
E. wichitorum	2017-34	34.72315	-98.69627	Comanche	2017	Yes	No	Yes	Yes	No
E. wichitorum	2017-36	34.7267	-98.59861	Comanche	2017	Yes	No	No	No	No
E. wichitorum	2017-37	34.71557	-98.63825	Comanche	2017	No	No	No	No	No
E. wichitorum	2017-38	34.73728	-98.72616	Comanche	2017	Yes	No	Yes	Yes	No
E. wichitorum	2017-39	34.6813	-98.63251	Comanche	2017	No	No	No	No	No
E. wichitorum	2017-40	34.68393	-98.63383	Comanche	2017	Yes	No	Yes	No	No
E. wichitorum	2017-41	34.6958	-98.63161	Comanche	2017	Yes	No	Yes	Yes	No
E. wichitorum	2017-42	34.70773	-98.73419	Comanche	2017	Yes	No	No	No	No

E. wichitorum	2017-43	34.70646	-98.70569	Comanche	2017	Yes	No	No	No	No
E. wichitorum	2017-44	34.73818	-98.52151	Comanche	2017	Yes	No	No	No	No
E. wichitorum	2017-45	34.73945	-98.51942	Comanche	2017	Yes	No	No	No	No
E. wichitorum	2017-46	34.74447	-98.51798	Comanche	2017	Yes	No	Yes	Yes	Yes
E. wichitorum	2017-47	34.7068	-98.68189	Comanche	2017	Yes	No	Yes	No	Yes
E. wichitorum	2017-48	34.81835	-98.79862	Comanche	2017	Yes	No	No	Yes	Yes
E. wichitorum	2018-1	34.75371	-98.57992	Comanche	2018	Yes	Yes	No	No	Yes
E. wichitorum	2018-2	34.73277	-98.53934	Comanche	2018	Yes	Yes	No	No	No
E. wichitorum	2018-3	34.71067	-98.62264	Comanche	2018	Yes	Yes	No	No	No
E. wichitorum	2018-4	34.73352	-98.72305	Comanche	2018	Yes	Yes	No	No	No
E. wichitorum	2018-5	34.72385	-98.71992	Comanche	2018	Yes	Yes	No	No	No
E. wichitorum	2018-6	34.72776	-98.70751	Comanche	2018	Yes	Yes	No	No	Yes
E. wichitorum	2018-8	34.69473	-98.67696	Comanche	2018	Yes	Yes	No	No	Yes
E. wichitorum	2019-1	34.75119	-98.63177	Comanche	2019	Yes	Yes	No	No	Yes
E. wichitorum	2019-4	34.45945	-98.57254	Comanche	2019	Yes	Yes	No	Yes	Yes
E. wichitorum	2019-5	34.85099	-98.6957	Caddo	2018	Yes	Yes	No	Yes	No
E. wichitorum	2019-6	34.44938	-98.34233	Comanche	2019	Yes	Yes	No	Yes	Yes
E. wichitorum	2019-7	34.68106	-99.15937	Jackson	2019	Yes	No	No	No	No
E. wichitorum	2019-9	34.87877	-98.36893	Caddo	2019	Yes	Yes	No	Yes	Yes
E. wichitorum	2019-10	35.03914	-98.28586	Caddo	2019	Yes	Yes	No	Yes	Yes
E. wichitorum	2019-11	35.09232	-98.61879	Caddo	2019	Yes	Yes	No	Yes	Yes
E. wichitorum	2019-13	34.3614	-98.15669	Cotton	2019	Yes	No	No	Yes	Yes
E. wichitorum	2019-14	34.73152	-98.70766	Comanche	2019	No	No	No	Yes	Yes
E. wichitorum	2020-1	34.74392	-98.97392	Kiowa	2018	Yes	No	No	No	Yes
E. wichitorum	2020-2	34.64256	-98.92081	Kiowa	2018	Yes	No	No	No	Yes
E. wichitorum	CW	34.62503	-98.6667	Comanche	2019	No	No	No	No	Yes
Euchemotrema sp.	2019-2	35.41052	-98.30563	Canadian	2019	No	No	No	Yes	Yes
Euchemotrema sp.	2019-3	34.96338	-98.06857	Grady	2019	No	No	No	No	Yes
Euchemotrema sp.	2019-8	35.24742	-98.52663	Caddo	2019	Yes	No	No	No	No
Euchemotrema sp.	2019-12	36.12885	-98.57569	Blaine	2019	No	No	No	Yes	Yes
Euchemotrema sp.	2020-3	34.59466	-97.67532	Stephens	2020	No	No	No	Yes	Yes
N/A	2017-35	34.73982	-98.60542	Comanche	2017	No	No	No	No	No
N/A	2018-7	34.68196	-98.67669	Comanche	2017	No	No	Yes	No	No
N/A	DUD1	34.56559	-99.07158	Tillman	2019	No	No	No	No	No
N/A	DUD2	34.59434	-99.02032	Tillman	2019	No	No	No	No	No
N/A	DUD3	35.74611	-99.71531	Roger Mills	2019	No	No	No	No	No
N/A	DUD4	36.49854	-99.58222	Woodward	2019	No	No	No	No	No
N/A	DUD5	36.45688	-99.29859	Woodward	2019	No	No	No	No	No
N/A	DUD6	35.33545	-98.2118	Caddo	2019	No	No	No	No	No
N/A	DUD7	35.32407	-98.21591	Caddo	2019	No	No	No	No	No
N/A	DUD8	34.79985	-99.2352	Jackson	2019	No	No	No	No	No
N/A	DUD9	34.2243	-98.05254	Jefferson	2019	No	No	No	No	No
N/A	DUD10	34.89801	-99.32777	Greer	2019	No	No	No	No	No
N/A	DUD11	34.89406	-99.29987	Greer	2019	No	No	No	No	No
N/A	DUD12	34.93813	-99.30107	Kiowa	2019	No	No	No	No	No
N/A	DUD13	34.97741	-99.3806	Greer	2019	No	No	No	No	No
N/A	DUD14	35.15794	-98.89794	Washita	2019	No	No	No	No	No
N/A	DUD15	34.88683	-99.20471	Kiowa	2019	No	No	No	No	No
N/A	DUD16	34.80307	-99.26173	Jackson	2019	No	No	No	No	No
N/A	DUD17	34.06235	-97.9774	Jefferson	2019	No	No	No	No	No

N/A	DUD18	34.88486	-99.50068	Greer	2019	No	No	No	No	No
N/A	DUD19	34.53825	-99.18615	Tillman	2019	No	No	No	No	No
N/A	DUD20	34.55256	-99.41728	Jackson	2019	No	No	No	No	No
N/A	DUD21	35.0053	-99.1278	Kiowa	2019	No	No	No	No	No
N/A	DUD22	34.97263	-99.33452	Greer	2019	No	No	No	No	No
N/A	DUD23	34.98652	-99.33468	Kiowa	2019	No	No	No	No	No
N/A	DUD24	34.992	-99.42451	Greer	2019	No	No	No	No	No
N/A	DUD25	34.87017	-98.19724	Caddo	2019	No	No	No	No	No
N/A	DUD26	34.81653	-98.10899	Comanche	2019	No	No	No	No	No
N/A	DUD27	35.91134	-98.40781	Blaine	2019	No	No	No	No	No
N/A	DUD28	34.6126	-98.38272	Comanche	2019	No	No	No	No	No
N/A	DUD29	34.21765	-98.40093	Cotton	2019	No	No	No	No	No
N/A	DUD30	34.61523	-98.70802	Comanche	2019	No	No	No	No	No
N/A	DUD31	34.53493	-98.8845	Tillman	2019	No	No	No	No	No
N/A	DUD32	34.64415	-99.01904	Kiowa	2019	No	No	No	No	No
Species ID Total = 106 (67, 5, 34)				**County 15**		**12 x 12 60**	**Log 14**	**Soil pH 34**	**DFA 28**	**DNA 21**

Natural History

Breeding. The observed egg-laying peak for both wild and laboratory colonies was in the spring, starting in mid-March and continuing through April. Wild snails brought into laboratory conditions breed readily and successfully, with several colonies increasing their populations to over 100 individuals and many maintaining stable, multi-generation populations of greater than 30 individuals for more than two years. Most laboratory colonies observed during the spring of 2018 had more eggs clutches than individuals, indicating that individuals either split their clutches or have multiple clutches in a season if conditions are favorable. A comparison of clutch sizes between species showed that *E. wichitorum* (mean ± SE of 4.69 ± 0.32 eggs per clutch) had significantly fewer eggs per clutch than *E. leai* (6.64 ± 0.58) (Fig. 6). It is unclear if *E. wichitorum* lays fewer eggs or is simply more likely to split its clutches. Both species tended to bury their clutches only a few millimeters into the soil, and it was not uncommon to observe clutches laid directly under a substrate like a wood chip or piece of lettuce in the captive colonies.

Breeding experiments comparing crosses of *E. wichitorum*, *E. leai*, and *Stenotrema labrosum* were inconclusive. Like most species of land snails, these snails are hermaphroditic (an individual is both male and female), so any two snails should be able to breed. A few pairs did have eggs, but few eggs hatched and led to apparently healthy offspring. This is likely because polygyrids are semi-colonial and may not breed when only one conspecific is present. Colonies with five individuals readily reproduce, but colonies of four or less individuals seem to be less successful. However, this was not tested robustly, and other factors could have affected our crosses or colonies with fewer than five founders.

Genetics. The Bayesian phylogenetic tree of individuals with two-gene coverage (sequence for both COI and LSU) showed a distinct separation of individuals that could be confidently assigned to *E. wichitorum* and *E. leai* (Fig. 11). However, individuals from populations of *E.* westOK snails near Anadarko and Apache had some individuals sort with *E. wichitorum* and some sort with *E. leai*. While there are several reasons this pattern can be observed, both populations are included in the range of *E. wichitorum* because most individuals strongly match the description of *E. wichitorum*, which is further supported by morphometric analyses (Cooper unpublished). All *E.* westOK individuals from the Carnegie grouped with *E. wichitorum* while those from Canton Lake all grouped with *E. leai* and both populations can be assigned to those species, respectively. The lone *E.* westOK from Waurika Lake sorted with *E. wichitorum*, as did individuals with only single-locus coverage (unpublished data) so this population can be designated as *E. wichitorum* as well. These initial data suggest that *E. wichitorum* populations from the core range or the Wichita Mountains and its drainages are a genetically distinct lineage, and no taxonomic revision is suggested for this species at this time.

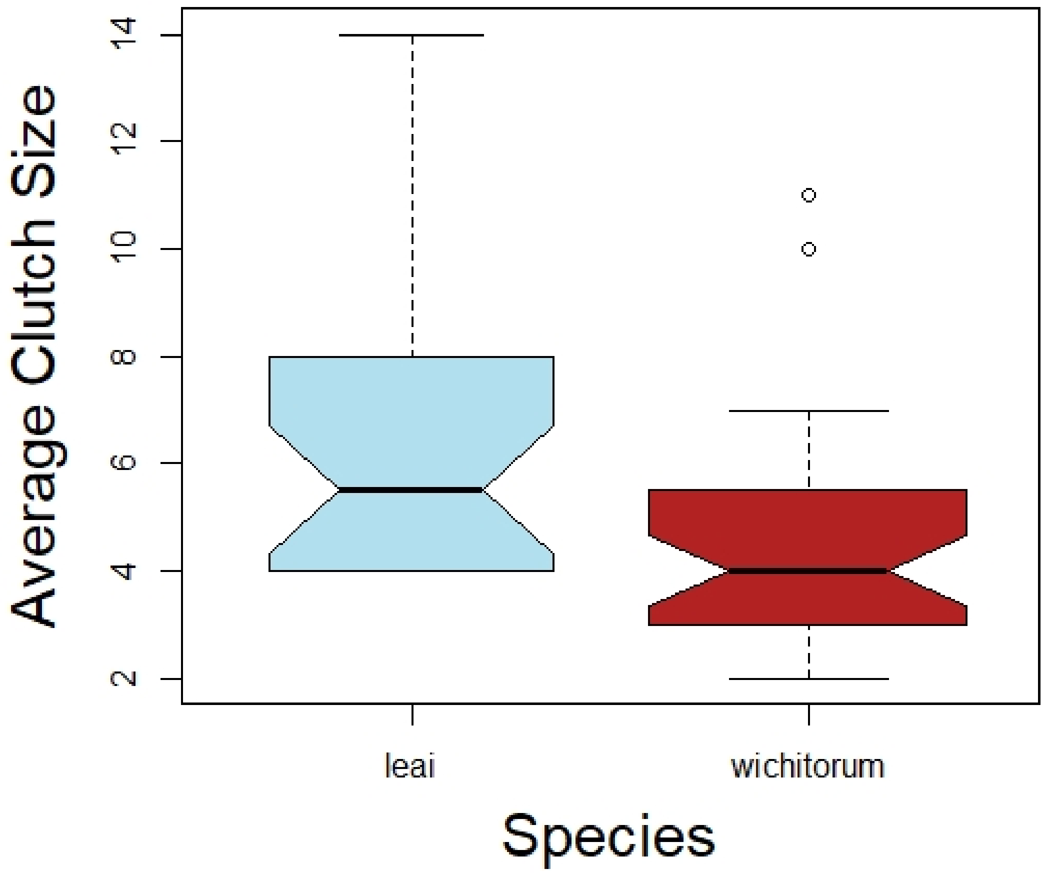

Figure 6: A comparison of clutch sizes (number of eggs per clutch) from five colonies of *E. wichitorum* and three colonies of *E. leai* from the first season the colonies were started. Colonies generally consisted of five founders. Black lines represent median values, with box width representing the relative sample size of each group and the notch representing the 95% confidence interval about the median. A Mann-Whitney U test showed that *E. wichitorum* had significantly smaller clutch sizes than *E. leai* ($P<0.01$). Most colonies had more clutches than founders.

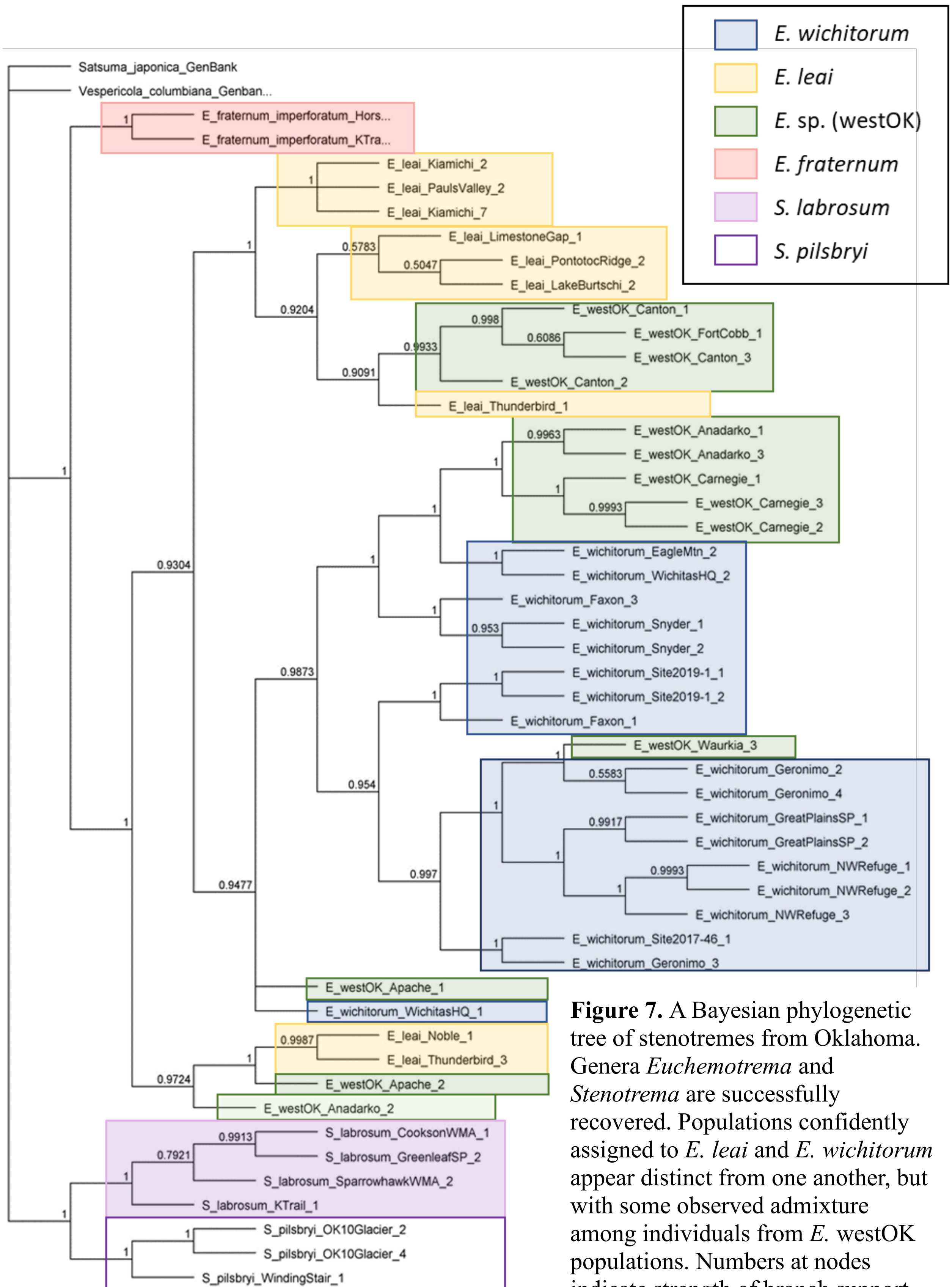

Figure 7. A Bayesian phylogenetic tree of stenotremes from Oklahoma. Genera *Euchemotrema* and *Stenotrema* are successfully recovered. Populations confidently assigned to *E. leai* and *E. wichitorum* appear distinct from one another, but with some observed admixture among individuals from *E.* westOK populations. Numbers at nodes indicate strength of branch support.

Table 2. Location data for all Oklahoma stenotreme populations used in our Bayesian phylogenetic tree. The _# after location name in the tree is a numbered identifier for each individual. E_ is for *Euchemotrema* and S_ is for *Stenotrema*. E_westOK represents populations that could not confidently be assigned to species level in the field at the time of collection. GPS coordinates are precise field measurements for all *E_wichitorum* and E_westOK populations, most of the others are approximated from Google maps.

Phylogeny Label	Locality	County	GPS
E_fraternum_imperforatum_HorseThief	Horse Thief Spring	LeFlore	34.73866, -94.72841
E_fraternum_imperforatum_Ktrail	K-trail of Indian Hwy	Pushmataha	34.68219, -95.05366
E_leai_Kiamichi	K-River Campground Kiamichi River	Pushmataha	34.34084, -95.63646
E_leai_LakeBurtschi	Lake Burtschi	Grady	34.96338, -98.06857
E_leai_LimestoneGap	Limestone Gap	Atoka	34.60173, -95.97708
E_leai_Noble	Ken Parker's Proerty, Noble	McClain	35.14154, -97.40470
E_leai_PaulsValley	Paul's Valley Lake	Garvin	34.76841, -97.20112
E_leai_PontotocRidge	Pontotoc Ridge	Pontotoc	34.52209, -96.60661
E_leai_Thunderbird	Lake Thunderbird	Cleveland	35.20611, -97.23551
E_westOK_Anadarko	Oak Ridge Camp, Anadarko	Caddo	35.03914, -98.28586
E_westOK_Apache	Tom Manar Bridge, US Hwy 62 S of Apache	Caddo	34.87877, -98.36893
E_westOK_Canton	Canton Lake WMA, off E0615 Rd	Blaine	36.12392, -98.57564
E_westOK_Carnegie	Off Hwy 9, SW Carnegie	Caddo	35.09232, -98.61879
E_westOK_FortCobb	Cobb Creek floodplain N of Fort Cobb Lake	Caddo	35.24742, -98.52663
E_westOK_Waurika	Waurika WMA, Beaver Creek floodplain	Cotton	34.36140, -98.15669
E_wichitorum_Site2019-1	Wichita Mountains Wildlife Refuge, 2019-1	Comanche	34.75119, -98.63177
E_wichitorum_Site2017-45	WMWR, 2017-45	Comanche	34.73945, -98.51942
E_wichitorum_Site2017-46	WMWR, 2017-46	Comanche	34.74447, -98.51798
E_wichitorum_EagleMtn	WMWR, Eagle Mtn	Comanche	34.69473, -98.67696
E_wichitorum_NWRefuge	WMWR, NW Corner	Comanche	34.81689, -98.83549
E_wichitorum_RefugeHQ	WMWR, E of refuge HQ	Comanche	34.73152, -98.70766
E_wichitorum_Faxon	E of Faxon, along W Cache Creek	Comanche	34.4594, -98.5725
E_wichitorum_Geronimo	SE of Geronimo, East Cache Creek	Comanche	34.44938, -98.34233
E_wichitorum_GreatPlainsSP	Great Plains State Park	Kiowa	34.74392, -98.97392
E_wichitorum_Snyder	Private Property SE of Snyder	Kiowa	34.85099, -98.69570
S_labrosum_CooksonWMA	Cookson State Game Refuge	Cherokee	35.67388, -94.83932
S_labrosum_GreenleafSP	Greenleaf SP	Muskogee	35.62277, -95.16760
S_labrosum_Ktrail	K-trail of Indian Hwy	Pushmataha	34.60219, -95.05366
S_labrosum_SparrowhawkWMA	Sparrowhawk WMA	Cherokee	35.95960, -94.90381
S_pilsbryi_OK10Glacier	State Hwy OK-10 Rock Glacier	LeFlore	34.68837, -94.62556
S_pilsbryi_WindingStair	Winding Stair Pulloff	LeFlore	34.68901, -94.55495

RECOMMENDATIONS:

The main management concern for individual populations of *E. wichitorum* is fire. Our general recommendation to minimize the negative impacts of fire while maximizing the potential benefits of fire (e.g., increased calcium availability) for snail populations is to mimic the historical fire interval of the Wichita Mountains. Historically, the most common fires in the Wichita Mountains were low-severity fires during the dormant season, approximately September to March (Stambaugh et al. 2009). Mimicking this historic fire regime should theoretically minimize snail mortality because low-intensity fires generally do not completely burn logs and generally leave a mosaic with a mixture of burned and unburned patches. Snails tend to survive fire if the log-soil interface of their shelter log remains intact and do not seem to be negatively affected by surface charring or partial burning of a section of their shelter log. Burning during the dormant season should also mean there are no eggs or young juveniles in the population, which are the two groups most likely to be negatively impacted by the drier environmental conditions immediately following a fire. Burned logs in the WMWR retain a layer of char for at least two years (Cooper, Pers. Obs.) and thus the influx of available calcium should continue to be present for snails during the early portion of the growing season, when this nutrient is most needed by adults for egg production and by snail hatchlings to grow their shells. Burning within several days of a rain event is also a potential concern. Given the generally mild winters of the WMWR, snails may become active and leave their shelter logs after a rain event, even in the winter. While any fire set in slightly damp conditions several days after a rain is likely to be a low-severity burn, it may kill snails that have left their shelter logs and temporarily moved into the leaf litter to forage. Conversely, burning during drought conditions can result in smoldering logs that can reduce logs to ash even during a low-severity burn.

Given the relatively novel finding that *E. wichitorum* populations may benefit from low-severity burns, a more direct study of the effects of fire on bioavailable nutrients, snail mortality, and post-fire recruitment would be informative for both this species' conservation and for developing the scientific understanding of the potential effects of fire on land snails more generally. Such a project could be done by setting up experimental plots where all snails in the plot are censused and marked for regular recapture. A portion of plots can be burned and monitored over the course of 2-5 years. A portion of plots could test potential snail abundance-promotion techniques, such as the addition of calcium-rich wood ash, the addition of more shelter logs, or the addition of different types of leaf litter to test if these actions increase snail abundance and might help populations recover after fire. The mark-recapture data also would provide data on movement patterns in this species and would help determine the species' average lifespan in the wild.

Additional population genetics work could be done to examine the genetic diversity and patterns of gene flow between *Euchemotrema* populations in western and central Oklahoma. This research could help delimit populations of uncertain taxonomy and establish a more defined range boundary between *E. wichitorum* and *E. leai*. Additional sampling efforts for such a project are also likely to expand the known range of both species. Population genetics data also may provide insights into the historical movement patterns of *Euchemotrema* into Oklahoma and the timing of the retreat of the Cross Timbers, which is the event most likely to have caused the isolation and subsequent divergence of *E. wichitorum* from *E. leai*.

Lastly, any additional research on the behavior of this species in the wild could influence conservation decisions. Behavioral observations of land snails tend to be done at night after or during rain events, because this is when they are most likely to be actively moving through their habitat. Given the abundance of large animals and visitors in the WMWR, such a project would be best suited to elsewhere in *E. wichitorum's* range where experiments could be better protected. Additionally, identification of a favored foods could help inform future survey efforts while understanding seasonal movement patterns could provide more granular information for when the species is most vulnerable to fire.

SIGNIFICANT DEVIATIONS:

For the genetics portion of the project, the proposal called for work to be done in the lab of Dr. Cam Siler at the Sam Noble Museum of Natural History. Genetics work was instead conducted at the University of Oklahoma Biology Core Molecular Lab because the availability of an in-house DNA sequencer and full-time technician reduced overall cost and streamlined workflow.

EQUIPMENT:

No equipment was purchased.

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