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## CHANGES IN THE COMMUNITY COMPOSITION OF RIVERINE SNAKES (SQUAMATA: SERPENTES) OVER FIVE DECADES

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**Abstract.**—Biodiversity has been rapidly declining worldwide for over 175 y, and there do not appear to be any particular ecosystems or taxonomic clades that are exempt from this trend. Habitat alteration is an ongoing threat to the quality of the upper-middle Brazos River in Texas, USA, and changes associated with impoundments have been especially persistent over the past century. We examined data from four discrete surveys that spanned a 53-y period to determine changes in the snake community along the upper-middle Brazos River. Community structure changed since 1968, with the numbers of species and individuals per species both fluctuating over time. Values for  $\alpha$ -diversity (number of species) over time indicate that, after declining, species richness has recently increased.  $\beta$ -diversity (community composition over a region) estimates, however, indicate that species turnover (80%), rather than nestedness (20%) within a richer community, was primarily responsible for changes in community diversity. High values of turnover indicate that species experiencing a bottleneck are unlikely to recover via dispersal events from adjacent communities. Temporal  $\beta$ -diversity indices reveal that the species still present in the surveyed section of the watershed have increased in abundance, indicative of potential homogenization of the community. Based on the estimated values for  $\alpha$ - and  $\beta$ -diversity, we suggest that the landscape of the upper-middle Brazos River needs management to sustain the richness of the snake community. Because diversity in this community is influenced primarily by species turnover, preservation of remaining riverine habitat and multiple protected sites along the river are needed to prevent the likely loss of additional species.

**Key Words.**—beta diversity; Brazos River; long-term data; riparian habitat; snake community

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### INTRODUCTION

Anthropogenic factors, such as habitat alteration and introduced species, have caused global biodiversity to rapidly decline over the past 175 y (Purvis et al. 2000; Araújo et al. 2006; Butchart et al. 2010; Sewell et al. 2012). Declines in species diversity reduce the complexity of ecological interactions, which can render an ecosystem less stable in the face of environmental change (*sensu* Hutchinson 1959). Ecosystems that contain endemic species are of particular concern because the habitat requirements for those species are unlikely to occur elsewhere, either naturally or through manipulation.

Species diversity on a local scale, or  $\alpha$ -diversity, can be useful when analyzing the changes in community structure over time (Wagner et al. 2018). Because it does not take into account taxonomic distinctness, however,  $\alpha$ -diversity might provide relatively little information about changes in species composition (Yuan et al. 2016; Buckland et al. 2017; de Fraga et al. 2018). For example,

a single community can experience a shift in species composition but could still retain the same  $\alpha$ -diversity (Wagner et al. 2018). For this reason,  $\beta$ -diversity (the variation in community composition among sites within a region; Whittaker 1972) is often used to infer patterns of diversity (Pickett et al. 1987; McEwan et al. 2011; Vellend 2016; Storniolo et al. 2019). Statistical methods to detect differences between estimates of  $\beta$ -diversity over time have only recently been developed (e.g., Legendre 2019). Temporal  $\beta$ -diversity was described by Legendre and Gauthier (2014) to analyze both gradual and abrupt temporal variations in community composition. Legendre (2019) expanded the utility of the index a step further by introducing temporal  $\beta$ -diversity indices to empirically examine changes in community structure over time. Temporal  $\beta$ -diversity indices have been used to explore patterns of  $\beta$ -diversity using a wide range of model organisms, including plants (Legendre and Condit 2019; Lindholm et al. 2020; Vale et al. 2021), invertebrates (Chen et al. 2020; Pereira et al. 2020; Correa et al. 2021; Dong et al. 2021), and

vertebrates (Kuczynski et al. 2018; Zhou et al. 2020; Liang et al. 2021).

$\beta$ -diversity also has important implications for conservation, because reductions in  $\beta$ -diversity can characterize homogenized communities and the subsequent loss of ecosystem function (Socolar et al. 2016). Various measures can quantify  $\beta$ -diversity, including phylogenetic  $\beta$ -diversity, functional  $\beta$ -diversity, and taxonomic  $\beta$ -diversity. Combinations of taxonomic  $\beta$ -diversity and functional  $\beta$ -diversity are appropriate for studies concerning community ecology and conservation because they have the potential to reveal the evolutionary, taxonomic, and ecological mechanisms that influence community structure (Devictor et al. 2010; de Fraga et al. 2018). All  $\beta$ -diversity measures can be partitioned into two ecological processes: turnover (i.e., species replacement; *bsim*) and nestedness (i.e., species gains and/or losses; *bsne*). Values for turnover and nestedness often differ (Baselga 2010), and each is influenced by different ecological and environmental phenomena (Bergamin et al. 2017; Fu et al. 2019). Identifying whether nestedness or turnover is the dominant process influencing the  $\beta$ -diversity value for a community is necessary because the processes have different responses to singular management practices (Baselga 2010).

Riparian zones are dependent on natural hydrologic disturbances that create spatially and temporally unique environmental conditions (Naiman and Décamps 1997). Hydrologic conditions can vary both over the course of a year and from one year to the next (Heede 1980). Despite only representing 2% of available habitat on the surface of the Earth, freshwater ecosystems have relatively high faunal community diversity when compared to marine and terrestrial communities (Román-Palacios et al. 2022). Freshwater species often constitute the majority of species present within a landscape (Thomas et al. 1979) and can be directly affected by environmental fluctuations characteristic of riparian areas. Threats, such as drought (Vogrinc et al. 2018) and habitat alteration (e.g., damming, overgrazing; Skalak et al. 2013; Scarpino 2018; Mahmoudi et al. 2021), can lead to population declines of species within a riparian zone.

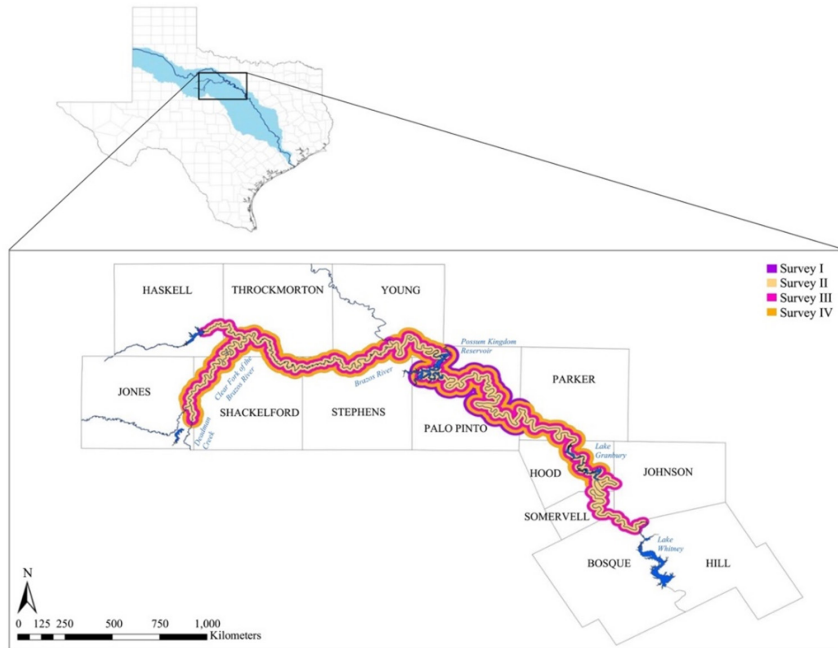
Despite their role as indicators of ecosystem function and health (Vitt 1987; Beaupre and Douglas 2009), there have been relatively few long-term studies monitoring snake communities and their responses to habitat disturbance (but see Fitch 1999; Sullivan 2000; Palis 2010; Crowshaw et al. 2019; Storniolo et al. 2019). The snake species occurring along the upper Brazos River in north-central Texas, USA, have experienced pressures at various temporal and spatial scales, such as extreme winter storms (National Oceanic and Atmospheric Administration. February 2021: Historic Winter Storm and Arctic Outbreak. National

Oceanic and Atmospheric Administration's National Weather Service. U.S. Department of Commerce, USA. Available at <https://www.weather.gov/fwd/Feb-2021-WinterEvent> [Accessed 18 August 2022]) and droughts (National Drought Monitoring Center. Historical Data and Conditions. National Drought Monitoring Center: U.S. Department of Agriculture, National Oceanic and Atmospheric Administration, and United States Drought Monitor, USA. Available from <https://www.drought.gov/historical-information?state=texas&dataset=2&selectedDatePaleo=2011&dateRangePaleo=2010-2012> [Accessed 18 August 2022]), and extensive damming (Texas Water Development Board. Texas Lakes & Reservoirs: History of Reservoir Construction in Texas. Texas Water Development Board, USA. Available at <https://www.twdb.texas.gov/surfacewater/rivers/index.asp> [Accessed 18 August 2022]). Although many of the taxa associated with the Brazos River are relatively common throughout the state, the ecosystem is also inhabited by rarer species (e.g., Brazos River Watersnakes, *Nerodia harteri*, one of two endemic snake species in Texas; Werler and Dixon 2000). Endemic taxa are known to be important indicators of community diversity (Dirzo and Raven 2003), but many endemic snake species, including *N. harteri*, have experienced disproportionate population declines when compared to sympatric species (Scott et al. 1989; Ceballos and Ehrlich 2002; McBride 2009).

The 10 natural regions (ecosystems) in Texas contain the highest level of snake diversity in the USA (Dixon 2000; Powell et al. 2016), so it is necessary to differentiate between short-term population fluctuations and long-term population declines and/or extirpations. Herein, we describe patterns of snake community diversity within the upper Brazos River watershed since 1968, using  $\alpha$ - and  $\beta$ -diversity estimates. Our goal is to both describe the temporal variation in the diversity of snakes occurring in this system, and provide baseline measures to inform future conservation efforts directed towards the snakes inhabiting this region.

### MATERIALS AND METHODS

We combined multiple sources of data (Porter 1969; McBride 2009; Harding 2022; Yates 2022; Norman Scott, unpubl. data; Appendix Table 1) to produce a dataset of snake species observed over a 53-y period within the middle reaches of the Brazos River basin, in north-central Texas, USA (Fig. 1), from 1968 to 2021. Survey design, effort, and methods differed between studies (Appendix Table 1), but all researchers recorded each snake species observed. Our intentions were not to follow exactly the sampling regime that had been employed by one or both of the earlier studies, particularly the upland component of Porter (1969). As



**FIGURE 1.** Map of the Brazos River in Texas, USA (shaded blue area of inset indicates watershed), with counties surveyed for snakes shown in more detail. Colored buffers represent extent of the river searched for snakes in each of four surveys spanning 1968–2021. See Methods and Appendix Table 1 for the details of each survey.

such, we acknowledge that differences in the designs of the studies included in our meta-analysis could explain perceived changes in the snake community over time. Data we analyzed came from four surveys (Appendix Table 1). There was at least one surveyor present during Surveys I and II, and at least two surveyors present during Surveys III and IV. The total amount of watershed surveyed was greatest during Surveys II and III, followed by Survey IV, and finally Survey I. Survey effort was greatest during Survey III (966.3 person-hours), followed by Survey IV (628.5 person-hours), and then Survey II (33.7 person-hours). Person-hours were not recorded during Survey I. The timing of surveys differed slightly between data sources, but survey effort was concentrated during the warmer months that coincided with greater snake activity (April to May and September to October). All surveys used active methods (e.g., canoe, kayak, etc.), and all but one (Survey II) also included passive methods (e.g., minnow traps). Reservoirs such as Possum Kingdom Reservoir and Lake Granbury were included in all but one survey (Appendix Table 1).

**Statistical analyses.**—We used the diversity function in the *vegan* package in R statistical software to estimate values of  $\alpha$ -diversity for each of the four time periods between the first year of the earliest study and the last year of the most recent effort (Okansen et al. 2020; R Core Team 2020). Taxonomic  $\beta$ -diversity and functional  $\beta$ -diversity were estimated using the *beta.multi* and

*functional.beta.multi* functions, respectively, from the *betapart* R package (Baselga et al. 2021). Temporal  $\beta$ -diversity was estimated using the TBI function in the *adespatial* R package (Dray et al. 2021), which tests temporal  $\beta$ -diversity dissimilarity indices between paired multivariate observations of time 1 (T1) and time 2 (T2), using the quantitative form of the Sørensen index (Sørensen 1948).

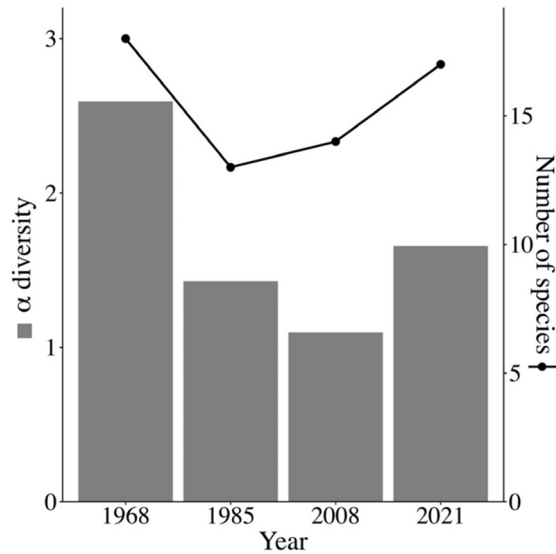
TBI calculates the vector of temporal  $\beta$ -diversity as:

$$(D = [B + C] / [2A + B + C]),$$

which is also the percentage difference between T1 and T2. A is the sum of  $A_j$  values for individual species ( $A_j = \min[y_{1j}, y_{2j}]$ ) and is the unscaled similarity between T1 and T2. B is the sum of  $B_j$  values for individual species ( $B_j = y_{1j} - y_{2j}$  if  $y_{1j} > y_{2j}$ ; otherwise,  $B_j = 0$ ) and is the unscaled sum of species loss between T1 and T2. C is the sum of  $C_j$  values for individual species ( $C_j = y_{2j} - y_{1j}$  if  $y_{2j} > y_{1j}$ ; otherwise,  $C_j = 0$ ) and is the unscaled sum of species gains between T1 and T2. For our analyses, T1 was represented by Surveys I and II (1968–1985) and T2 was represented by Surveys III and IV (2006–2021).

## RESULTS

From 1968 to 2021, we found 1,698 individuals from 25 species representing three families (Appendix Table 2). Watersnakes (*Nerodia* spp.) were the most frequently observed snakes, followed by Western Ribbonsnakes

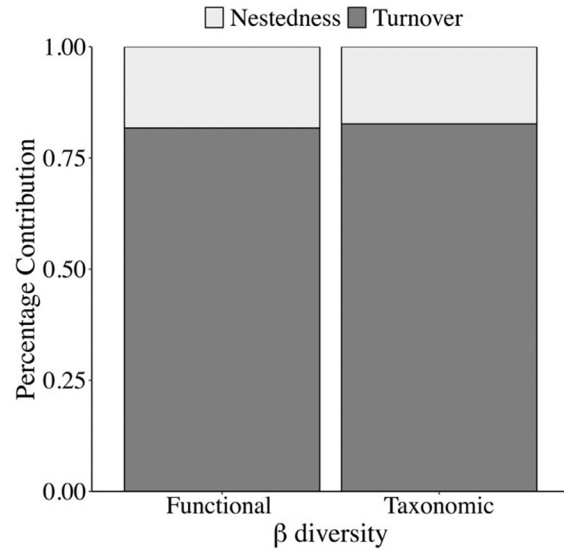


**FIGURE 2.**  $\alpha$ -diversity (left y-axis) and number of species observed (right y-axis) during surveys of the snake community associated with the Brazos River, Texas, USA, from 1968–2021.

(*Thamnophis proximus*) and Western Diamond-backed Rattlesnakes (*Crotalus atrox*). The total number of individual snakes observed increased from Survey I to Survey III, but decreased during Survey IV. The number of species observed was highest in Survey I, was lower during Surveys II and III, before rebounding during Survey IV (Fig. 2). The value for  $\alpha$ -diversity decreased from Survey I to Survey III, but increased during Survey IV (Fig. 2). Patterns of species turnover and nestedness were similar for taxonomic  $\beta$ -diversity ( $\beta_{sim} = 82.66\%$ ,  $\beta_{sne} = 17.34\%$ ) and functional  $\beta$ -diversity ( $\beta_{sim} = 81.73\%$ ,  $\beta_{sne} = 18.27\%$ ; Fig. 3), with turnover being the primary contributor to values of either functional or taxonomic  $\beta$ -diversity. Temporal  $\beta$ -diversity indices did not show significant changes within T2 (Surveys III and IV;  $P = 0.900$ ), however, they did show significant changes within T1 (Surveys I and II;  $P = 0.048$ ). The temporal  $\beta$ -diversity values did not indicate substantial changes in species composition between T1 and T2, but rather suggested that the community increased in abundance per species between T1 and T2 (Table 1).

**TABLE 1.** Temporal  $\beta$ -diversity indices (TBI) for the snake community associated with the Brazos River, Texas, USA, based on the percentage difference (D) between surveys of time 1 (T1) and time 2 (T2), estimated as a function of unscaled similarity between surveys (A), unscaled sum of species losses between surveys (B), and unscaled sum of species gains between surveys (C). Any increase in abundance per species is indicated by + in the change (D) column. See Methods for the time periods included in T1 and T2.

Time	D ( $([B + C] / [2A + B + C])$ )	$p_{TBI}$	$\Delta$
T1	0.913	0.048	+
T2	0.497	0.900	+



**FIGURE 3.** Percentage contribution of nestedness and turnover to two forms of beta diversity: functional  $\beta$ -diversity and taxonomic  $\beta$ -diversity.

## DISCUSSION

Because snakes have been the subject of few long-term community studies (Parker and Plummer 1987; Vitt 1987), any such data are valuable for future conservation work. For example, it was only through a 21-y study that Storniolo et al. (2019) were able to identify slight, but significant fluctuations in the composition of a snake community. Prior to our meta-analysis, there had been no consideration of changes in the snake community within the upper-middle Brazos River watershed over any length of time. Although the study design and effort differed between each of the surveys examined here (i.e., number of surveyors, amount of watershed surveyed, etc.), our results indicate that the snake community within the middle reaches of the Brazos River has shifted over the course of 50 y. Specifically, fewer species are now observed, and more individuals of those remaining species are detected.

For three of the projects contributing to our meta-analysis, the majority of effort surveying the snake community was focused on *Nerodia harteri*. Thus, it is not surprising that watersnakes were the most frequently detected type of snake across all studies. Despite a bias in search effort towards *N. harteri*, certain other species (e.g., *Crotalus atrox*, *Thamnophis proximus*) seem to have become more abundant over time. Other species observed during earlier surveys were absent in the later efforts, a pattern that is as likely an outcome from the loss of generalist species that are expected to be present (e.g., Eastern Hog-nosed Snakes, *Heterodon platirhinos*) as it is from the reduced focus towards upland species (e.g., Long-nosed Snakes,

*Rhinocheilus lecontei*, Flat-headed Snakes, *Tantilla gracilis*, Lined Snakes, *Tropidoclonion lineatum*) during later surveys compared to earlier surveys. These trends are consistent with those observed in other long-term community studies (e.g., Fitch 1999; Ernst et al. 2016; Crowshaw et al. 2019). Snake species do not respond to environmental changes equally. Surveys in Carolina Bay habitat revealed a post-drought increase in the number of Northern Cottonmouths (*Agkistrodon piscivorus*), whereas *Nerodia* spp. appeared to be vulnerable to local extinctions over time (Willson et al. 2006). Seigel et al. (1998) also documented similar population shifts that varied by species in response to changing hydrological conditions. Our results indicate that certain snake taxa (e.g., *Nerodia* spp., *Thamnophis* spp.) are better adapted to the changing conditions of the Brazos River, whereas other snake species (e.g., *Tantilla gracilis*, *Tropidoclonion lineatum*) might not respond as well to changes in their respective resource bases (*sensu* Willson et al. 2006).

Values for  $\alpha$ -diversity declined from 1968 to 2008, but increased in the most recent survey efforts. This pattern would typically imply an improved community structure, except that turnover (not nestedness) was primarily responsible for patterns in  $\beta$ -diversity. Proportionately high turnover indicates that patterns of community change over time within the Brazos River were influenced by environmental factors, competition, and geographical barriers, rather than those phenomena that influence nestedness (i.e., extinction and colonization; Bergamin et al. 2017; Fu et al. 2019). Based on low values for nestedness, we suggest that the snake community within the Brazos River watershed is not simply a subset of a larger biogeographic region. Furthermore, any species lost from the Brazos River community are not likely to be replaced by recruitment events from outside that ecosystem (Wright and Reeves 1992; Ulrich and Gotelli 2007). A lack of such immigration events could be attributed to reduced lateral fluvial influence from adjacent wetlands in the Brazos River watershed. Because of this isolation from nearby landscapes, the watershed is characterized by repeated geologic faunal restrictions (Cummins 1908; Nelson et al. 2013).

Different values for temporal  $\beta$ -diversity indicate that species composition changed between Survey I and Survey II. When comparing species compositions between Surveys I and II (T1) and Surveys III and IV (T2), however, temporal  $\beta$ -diversity values indicated that those snake species still present within the Brazos River watershed have increased numbers of individuals, indicating that the snake community is trending towards homogenization (Socolar et al. 2016). Homogenous communities are disproportionately affected by environmental disturbances (Olden et al. 2004), which

might result in local extinctions and the loss of specialist species (Scheiner 2002). Within a given community, any specialist species lost could be replaced by generalist species resulting in functional homogenization and decreased community viability (Olden et al. 2004; Olden 2006; Clavel et al. 2010).

Communities containing endemic species are a conservation priority (Pressey et al. 1993). Therefore, continued monitoring of the Brazos River snake community is warranted to help prevent any further loss of species and their respective functional roles in the ecosystem (Bracken and Low 2012). Increased individuals per species, combined with high turnover contributions to taxonomic  $\beta$ -diversity and functional  $\beta$ -diversity, suggest that the complexity of the Brazos River snake community has declined since 1968. Despite dramatic declines and even multiple local extirpations that followed a severe drought, Willson et al. (2006) reported that populations of *Nerodia* spp. re-established through dispersal events from other wetland habitats. If a snake species occurring within the Brazos River watershed has declined in abundance and can recover through similar dispersal events, community complexity, and thus stability, would increase (Hutchinson 1959), thereby promoting the persistence of multiple snake species, including the Texas endemic *Nerodia harteri*. We suggest that protection of multiple sites along the Brazos River (but see Li et al. 2021) and preservation of the remaining riverine habitat are both necessary to prevent the continued loss of species.

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**APPENDIX TABLE 1.** Qualitative and quantitative data of surveys of the upper-middle Brazos River, located in north-central Texas, USA, that comparatively illustrate difference in sampling period, extent of watershed surveyed, minimum number of surveyors (Min. no. of surveyors), and techniques used (see Methods). Survey labels are referenced in the narrative.

Survey label	Source	Survey period	Earliest and latest month surveyed	River Reach (upstream limit, UL; downstream limit, DL)	Total watershed encompassed by surveys (km)	Min. no. of surveyors	Reservoirs included in surveys	Survey methods
I	Porter (1969)	1968–1969	February July	UL: Morris Sheppard Dam, Palo Pinto County DL: Eastern boundary of Palo Pinto County (Soda Springs)	130	1	No	Active Passive
II	Norman Scott, unpubl. data	1984–1985	April October	UL: Clear Fork in Jones County and Paint Creek near Lake Stamford DL: Cedar Creek, Hill County	873	1	Yes	Active
III	McBride (2009)	2006–2008	April October	UL: Deadman Creek near PR 362, Jones County, and Paint Creek near Loop Rd., Haskell County DL: Ham Creek Park, Johnson County	760	2	Yes	Active Passive
IV	Harding (2022) Yates (2022)	2018–2021	March October	UL: Deadman Creek, Jones County DL: Lake Granbury, Hill County	242	2	Yes	Active Passive

**APPENDIX TABLE 2.** Number of individuals per snake species observed during surveys of the Brazos River watershed, Texas, USA, across four survey periods.

Clade/Species	Common Name	Survey			
		I	II	III	IV
Leptotyphlopidae					
<i>Rena dulcis</i>	Texas Threadsnakes	1	--	--	2
Viperidae: Crotalinae					
<i>Agkistrodon contortrix</i>	Eastern Copperheads	3	3	2	4
<i>Agkistrodon piscivorus</i>	Northern Cottonmouths	1	--	2	3
<i>Crotalus atrox</i>	Western Diamond-backed Rattlesnakes	2	8	--	16
Colubridae: Colubrinae					
<i>Coluber constrictor</i>	North American Racers	4	1	3	1
<i>Coluber flagellum</i>	Coachwhips	4	--	--	4
<i>Lampropeltis (getula) holbrooki</i>	Speckled Kingsnakes	1	--	1	--
<i>Ophedrys aestivus</i>	Rough Greensnakes	3	--	1	--
<i>Pantherophis emoryi</i>	Great Plains Ratsnakes	1	--	1	7
<i>Pantherophis obsoletus</i>	Western Ratsnakes	2	4	9	4
<i>Pituophis catenifer</i>	Gophersnakes	2	2	--	2
<i>Rhinocheilus lecontei</i>	Long-nosed Snakes	--	2	--	--
<i>Salvadora grahamiae</i>	Eastern Patch-nosed Snakes	--	--	--	5
<i>Sonora semiannulata</i>	Western Groundsnakes	--	--	1	--
<i>Tantilla gracilis</i>	Flat-headed Snakes	2	--	--	--
Colubridae: Dipsadinae					
<i>Heterodon platirhinos</i>	Eastern Hog-nosed Snakes	1	2	--	--
Colubridae: Natricinae					
<i>Haldea striatula</i>	Rough Earthsnakes	--	3	--	3
<i>Nerodia erythrogaster</i>	Plain-bellied Watersnakes	10	52	253	92
<i>Nerodia harteri</i>	Brazos River Watersnakes	1	168	42	123
<i>Nerodia rhombifer</i>	Diamond-backed Watersnakes	9	27	421	256
<i>Regina grahamii</i>	Graham's Crawfish Snakes	--	--	1	--
<i>Storeria dekayi</i>	Dekay's Brownsnakes	2	--	--	3
<i>Thamnophis marcianus</i>	Checkered Gartersnakes	--	22	1	1
<i>Thamnophis proximus</i>	Western Ribbonsnakes	4	--	17	69
<i>Tropidoclonion lineatum</i>	Lined Snakes	--	1	--	--
Total individuals		53	295	755	595
Total species		18	13	14	17